IMPROVING A TOMATO GROWTH MODEL TO PREDICT FRESH WEIGHT AND SIZE OF INDIVIDUAL FRUITS

By

MARIA RAQUEL RYBAK

A DISSERTATION PRESENTED TO THE GRADUATE SCHOOL
OF THE UNIVERSITY OF FLORIDA IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

UNIVERSITY OF FLORIDA

2009

To my Family

ACKNOWLEDGMENTS

I wish to express my thanks and compliments to my supervisory committee, Dr. Kenneth Boote, Dr. James Jones, Dr. Jerry Bennett, Dr. Eduardo Vallejos and Dr. Barry Tillman for being part of my committee and reading and criticizing the manuscript. I also owe appreciation to Dr. Bennett, who was my first contact at the University of Florida and diligently connected me with my advisor. My most considerable debt is to Dr. Kenneth J. Boote who was generous with his time and expertise in this research. His knowledge, patience and constant support were equally important to the completion of this dissertation.

In the academies one finds many intelligent professors but my honor and privilege has been to find two wise professors. My admiration and gratitude go to Dr. Ken Boote and Dr. Jim Jones, now and always.

Special thanks go to Dr. Johan Scholberg and Cheryl Porter for their indispensable help. They generously donated hours of time and shared valuable data with me. I also want say thank you to Dr. Lincoln Zotarelli, Dr. Michel Dukes, Mr. Wayne Williams, Mr. Richard Fethiere and Mr. Jason Hupp for their technical assistance. Sincere gratitude is extended to the faculty, staff members and other people in the Agronomy Department for the help they extended anytime I needed it.

I owe gratitude to the National Institute of Agricultural Technology in Argentina for authorizing and assisting me in this program. Especially thanks go to Ing. Nestor Oliveri who has supported me throughout my career.

Thanks to my family; they fill my heart with unimaginable love. Especially thanks to my beloved mother, Veronica and sister, Myrian. They are also my best friends and a source of constant encouragement. Myrian is always guiding my steps down a path that I can follow with confidence because she has been there before. My brothers, sisters and nephews are true gifts in

my life. I also want to honor the precious memory of my father. His love, integrity and wisdom always kept me going in the right direction.

I would like say thanks to Nidia, Carmen and Luca who have been as my own family in Gainesville. My memories go to my friend, McNair, who is gone but his example and kindness will be in my heart forever. Also thanks go to Sara Jane, Welch and Julie who gave me so much warmness.

Thanks to my friends who gave me motivation from distant lands, and those I met here who shared their friendship with me. Finally and always, thanks to my unfailing and amazing God for his everlasting love and grace which sustain me.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Abstract of Dissertation Presented to the Graduate School
of the University of Florida in Partial Fulfillment of the
Requirements for the Degree of Doctor of Philosophy

IMPROVING A TOMATO GROWTH MODEL TO PREDICT FRESH WEIGHT AND SIZE OF INDIVIDUAL FRUITS

By

Maria Raquel Rybak

May 2009

Chair: Kenneth J. Boote
Major: Agronomy

A new version of the CROPGRO-Tomato model was developed to include a subroutine for predicting dry matter concentration, fresh weight and size of fruits over time. This subroutine builds on already existing crop model predictions of dry mass per fruit and fruit thermal age. The model was calibrated with field data obtained on tomato cultivar 'Florida 47' in Gainesville Florida during spring 2007 and evaluated with an independent data set obtained during spring 2006. The dynamics of dry weight accumulation, fresh weight, dry matter concentration, and fruit size were simulated by the model and compared with independent data of fruits tagged at anthesis in the field study at three successive weekly dates. These results demonstrated that the model was able to explain and predict the time-series growth and development of individual fruits on a cohort basis, to include delayed growth, slower growth, and smaller size of progressively later-set fruits. Overall, the standard deviation of model error was less than 20 percent of the mean for all the variables evaluated (dry weight, fresh weight, fruit dry matter concentration, and fruit size). In addition, the Willmot index was always above 0.9.

The effects of water and N stress on the growth of individual fruits were studied by withholding drip irrigation for three periods and withholding N supply beginning at 14 days after transplanting. The main effects of water stress on the growth of individual fruits were reduced

fresh mass and size and an increase in dry matter concentration, while N stress on the other hand, caused a decrease in dry matter concentration of fruits. The existing water and N stress factors in the CROPGRO model were linked to the new equations that affect dry weight growth and dry matter concentration of individual fruits, and were successfully used to predict the stress-induced variations in dry matter concentration, and reductions in dry and fresh weight growth and size of single fruits. The newly-added subroutine for predicting dry matter concentration, fruit fresh weight, and size, along with coupling to water and N stresses make the improved model a valuable risk assessment tool for predicting fresh market production and quality of tomato.

CHAPTER 1
INTRODUCTION

Tomato production in Florida contributes greatly to the economy of the state. The total production in the US for the 2006-07 season totaled 13,524,530 million tons (11,484,800 tons processing tomatoes and 1,679,730 tons fresh market) from 175,150 hectares planted (126,910 hectares processing and 48,240 hectares fresh market). Florida accounted for 39 percent of the total U.S. tomato fresh production, followed by California with 33.2 percent. Eleven other states such as Georgia, Virginia and Ohio, accounted for the remaining 27.8 percent (Foolad, 2007). The value of the 2006-07 U.S. tomato crop was $2.05 billion, and of this $1.277 billion corresponded to fresh market, as published by the USDA's Statistical Service (Foolad, 2007).

The yield of vegetables for fresh market is usually defined by plant/fruit fresh weight, which is directly related to dry weight production (Marcelis *et al*., 1998). However, the relationship between growth in fresh matter and dry matter is poorly understood (Marcelis and Gijzen, 1998). A general process of prediction of fresh weight, comparable to the photosynthesis-based process used in mechanistic models for dry matter growth, is needed (Heuvelink *et al*., 2004).

Several models using tomatoes have focused on the carbon balance that leads to prediction of fruit growth on the basis of dry mass. Most of these are used for the purpose of growth and development studies and for the control of greenhouse environments. Some examples are TOMGRO (Jones *et al*., 1991), TOMSIM (Heuvelink and Bertin, 1994), TOMPOUSSE (Gary *et al*., 1997) and CROPGRO, in which tomato was one of the species included (Scholberg *et al*., 1997).

When fresh vegetables are the crops to be modeled, the photosynthesis-based models need to be modified, taking into consideration the high water content of these crops. For fresh

vegetables, the flow of water and carbon into individual harvestable organs dictates growth. However, most models simulate water relationships for the whole canopy based on the hydric balance of the soil-plant-atmosphere continuum. Moreover, fresh vegetables such as indeterminate tomato have cyclic patterns of yield influenced by the environment, and this variability has not been well modeled despite the potential practical application. On the other hand, the photosynthesis-driven models like CROPGRO have many advantages. Among these advantages is the fact that CROPGRO has been validated sufficiently for use in Florida. This is important considering that Florida is the leading producer state of fresh tomatoes in the USA, and CROPGRO has robust mechanistic support. It is desirable to know how, starting with the carbon balance, models like CROPGRO can be improved in order to develop practical applications for growers concerned with the prediction of fresh weight, graded size, and weekly yield variability of fresh market crops like tomato.

The general purpose of this work is to improve the existing CROPGRO-tomato model through the fulfillment of the following objectives:

- To update parameters in CROPGRO based on recent published literature.
- To investigate the functional relationships between fresh weight and dry weight growth of tomato fruits under different growth conditions.
- To develop a sub-model to simulate the fresh weight and the size of individual fruits on a cohort basis, and to validate the model with independent data.

CHAPTER 2
LITERATURE REVIEW

Introduction

Mechanistic crop models are valuable tools of research and can be used to integrate most of our knowledge of crop behavior (Acock and Reynolds, 1989; Heuvelink, 1995). In addition, validated models are well suited for predicting harvest time, a piece of information which is essential for optimal crop management and commercial planning strategies. Although CROPGRO-Tomato is one of the most complete models developed for tomato since it was developed more than 10 years ago, no further improvements or validations have been done. In this chapter a bibliographical review of research related to how environmental factors such as radiation, temperature, water and nutrients influence the growth and development of tomato is presented. The focus is on those functional relationships that could be useful for improving tomato modeling. In addition, genetic traits related to tomato yield are briefly reviewed. Moreover, a short section is devoted to describe the state of art of tomato models and related topics. General aspects about the species are not covered but some comprehensive text books are available that describe deeply the taxonomic, morphological and physiological traits of the species as well as production systems. Examples are: The tomato crop: a scientific basis for improvement (Atherton and Rudich, 1986), Cultivo del Tomate (Nuez, 1995) and more recently Crop Production Science in Horticulture: Tomatoes (Heuvelink, 2005).

Influence of the Environment on Growth and Development of Tomato Plants

Light

Light interception: The light is the most important factor affecting the productivity of tomato and a complete review was written by Papadopoulos and Parajasingham (1997). Heuvelink (1995) found that the average tomato crop growth rate is highly related ($R^2 = 0.87$; p

< 0.001) to the photosynthetically active radiation (PAR). From a practical point of view, the incident light may be less important in open field, where normally there are less light limitations as opposed to greenhouses; this is because the tomato specie is affected by chilling injuries and therefore shorter days typical of winter are normally avoided. Consequently, when the tomato is grown in open field, issues regarding the light interception may be more important than the incident radiation per se. The light measurement for photosynthesis is expressed as photosynthetic photon flux density (PPFD) in the range wavebands corresponding to 400-700 nm (Gardner, 1985).

For calculating the intercepted radiation it is accepted that light is exponentially attenuated within a canopy according to a function which derives from optical laws. This is expressed in general as $I/I_0 = e^{-kLAI}$ where I and I_0 are the total PPFD within and above the canopy, LAI is the leaf area index above I and k is the extinction coefficient (Gijzen, 1992), Acock *et al.* (1978) found that the k value for tomato is equal to 0.63 for the upper leaf layers and the stem, and it decreases to 0.52 deep in the canopy. Scholberg *et al.* (2000) reported that k values dropped from 1 early in the season to about 0.2 when the fully canopy was developed. The idea of making k variable throughout the season in tomato models has not been incorporated, and most models use a typical k value equal to 0.75 (CROPGRO) or 0.72 (TOMSIM) or some value in between. Therefore, performing sensitivity studies about k could be useful in order to improve the simulation of intercepted light.

The concept of LAI is normally applied for estimating the PPFD interception but the tomato canopy is usually structured in row arrangements. This has important consequences on light interception. In the first place, the edge of the canopy row receives additional PPFD from the sides (Gijzen, 1992), second the canopy is confined to discrete rows so different leaves at a

given depth can receive different amounts of radiation (Longuenesse *et al*., 1993). Last, the practice of tying the plants may limit its expansion and not all the assigned space is truly occupied by plants. Wilson *et al*. (1992) measured the light interception of a tomato canopy growing in greenhouse. They found that the interception of incident PPFD on the top of the canopy was 76 % while about 20 % was lost through gaps between rows. Simultaneously an average of 13 % reflectance and 23 % transmittance of the incident PPFD by the tomato canopy was determined. Several experiments about light penetration into a tomato canopy as a function of height for different plant spacing were carried out by Papadopoulos and Omrod (1988a). According to their results the proportion of available PPFD intercepted increased with closer spacing, but the vertical distribution of PPFD was better (more uniform) with wider plant spacing. Moreover, the effects of plant spacing were less important in spring than in autumn and they attributed these results to different growth stages of the crop which impact the extinction coefficient k. The authors argued that closer spacing was only important in the early part of the season but when enough LAI is developed the crop will intercept most of the available PPFD regardless of the initial spacing. Harper *et al*. (1979) found that tomato plants planted in autumn intercepted 30-40 % of incident radiation; by contrast, about 70 % of the radiation was intercepted by the plants in spring. Also, Papadopoulos and Omrod (1988a) found a closer relationship between LAI and PPFD interception than directly to plant density; therefore, interpretation of the Harper *et al*. (1979) data is difficult because they did not separate the effect of the season on the growth stage of the plant from the plant spacing effect. Scholberg *et al*. (2000) reported that even with fully developed canopy, field grown tomato only intercepted 50 to 60 % of the incident light due to the wide space between rows which resulted in an incomplete ground cover. Efforts have been made to improve the simulation of PPFD interception when the

crops are grown in rows. The concept of effective LAI for example was used by Acock (1991) where the effective LAI is the ratio between crop leaf area and shaded area and where the shadow area is simulated as a function of the shadow length measured at right angles to the row, the height of the crop row and the apparent solar elevation at right angles to the row (Gijzen, 1992). The advantage of this approach is that it is simple but it does not account for the PPFD scattering within the canopy so the light distribution is not well simulated. A more sophisticated improvement was proposed by Boote and Pickering (1994) to simulate PPFD interception by row crops. They incorporated the concepts of sun leaves (intercepting direct solar radiation) and shade leaves (intercepting scattered radiation originated from non-sun angles). The shadow projected by the canopy according their model is a function of the canopy dimensions (height and wide), latitude and azimuth angle, day of the year and time of the day. Using this shadow projection LAI is allowed to intercept PPFD and is assumed that the soil shaded by the plant canopy is the ground area occupied by the plant for photosynthesis. Likewise, the Gijzen and Goudriaan (1989) model was developed for simulating light distribution and photosynthesis in row crops.

Photosynthesis: The reported relationship between solar radiation and net photosynthesis is that photosynthesis initially increases linearly with irradiance level until the relationship becomes asymptotic (Papadopoulos, 1985; Longuenesse *et al*, 1993). The saturation level for photosynthesis inside greenhouse is 170 W m^{-2} (Papadopoulos and Omrod, 1988b) or ranges between 100 to 150 W m^{-2} (Cockshull, 1988), respectively. Outdoors, the values of saturating irradiance for photosynthesis reach 210 W m^{-2}, likely higher because of a higher CO_2 concentration. Furthermore, Gijzen (1995) determined that for closed canopies photosynthesis did not saturate up to 2000 µmol m^{-2} s^{-1}. Acock *et al.* (1978) reported that in tomato the upper

layer, which represented 23 % of the leaf area, assimilated the 66 % of the net CO_2 fixed by the canopy. In addition, a reduction from 8.6 to 5.2 in the leaf area index did not affect significantly the rate of net photosynthesis. However, when LAI was reduced to 2 (removing the middle leaves), the canopy photosynthesis was reduced by one third and the dark respiration by one quarter. These authors also measured the photosynthesis rate of individual leaves at upper, middle and lower layers of the canopies and concluded that the differences should be attributed to different amounts of light intercepted and not to leaf age differences. Papadopoulos and Omrod (1988b) reported that tomato plant spacing had a negligible effect on net photosynthesis of upper leaves but net photosynthesis of lower leaves was reduced for plants at a narrow spacing. In addition, photosynthesis is not a linear function of irradiance, but rather a non linear function with dependence on the nitrogen concentration of the leaves which have a saturating response to increased nitrogen concentration except at high irradiance level. This reveals the role of N on the Calvin cycle enzymes and the thylakoids which represent the majority of the leaf N content (Dewar, 1996).

Growth: The crop growth rate of tomato is directly related to the net assimilation rate and the leaf area index. The crop growth rate (CGR) is defined as the product of the net assimilation rate multiplied by the leaf area index (LAI) (Hunt, 1982). The PPFD interception is closely related to an early development of LAI. A fast covering of ground by leaves in tomato rows can be accomplished by optimizing the plant population (Harper *et al*., 1979; Papadopoulos and Omrod, 1990). According to Scholberg *et al*. (2000), tomatoes growing in open field reached a maximum LAI equal to 3.8 about 11 weeks after transplanting. The near optimal light interception occurred about 4 weeks after transplanting for plants spaced 45 cm in the row while at 60 cm the near optimal interception occurred 6 weeks after transplanting. Growth can also be

expressed as relative crop growth rate (RGR) which is the rate of gain in biomass in relation to the total biomass. The RGR is the product of the net assimilation rate (NAR) multiplied by the leaf area ratio (LAR), which in turn is defined as the leaf area for a given total biomass available for photosynthesis or leaf leafiness (Hunt, 1982). Bruggink and Heuvelink (1987) determined that for tomato the relationship between PPFD and RGR is well represented by a rectangular hyperbola and therefore at low daily light integrals the RGR will decrease. They simulated the growth of tomato plants and found that increasing NAR increased RGR.

Hurd and Thornley (1974) observed that high light integrals induced a decline in specific leaf area (SLA). They determined a SLA equal to 0.069 m^2 g^{-1} at 0.58 MJ m^{-2} day^{-1} and equal to 0.015 m^2 g^{-1} at 9.5 MJ m^{-2} day^{-1} in plants of 21 to 30 days age, and attributed these results to a differential biomass partitioning within leaves at high light integrals. In other words if the leaf thickness increases due a low sink source relationship the result will be a lower SLA. Similarly, Gary *et al*. (1993) found a negative correlation between tomato SLA and the mean light integral of the previous 3 days. In commercial practices De Koning (1993) measured a LAI equal to 3 in May but then he observed a linear decrease until it reached 1 in October. The SLA also decreased from 250 cm^2 g^{-1} in full grown leaves during spring to 100 cm^2 g^{-1} in summer. An average value of SLA for tomato equal to 196 cm^2 g^{-1} was reported by Heuvelink (1995). The seasonal variation in SLA is difficult to explain because several factors influence it at the same time. Ontogenetic changes, environmental influences (light, temperature, CO_2) and sink source effects are involved in these variations (Gijzen., 1992). The SLA can be expressed also as the inverse, which is called specific leaf weight (SLW or 1/SLA) in g m^{-2}. The SLW according to Papadopoulos and Omrod (1988b) decreases when the plant spacing is reduced. They found that the tomato SLW was 59 and 29 g m^{-2} in plants spaced at 45 and 23 cm, respectively, for plants

inside greenhouse. In plants outdoors and spaced at 30 cm the SLW was 32 g m^{-2}. According to these results, increasing the integral radiation in tomato can increase RGR via its effects on SLW of new leaves, which in turn increases NAR.

Yield: The slope of the relationship between crop biomass and intercepted light is usually referred as radiation use efficiency (RUE) which on average has a value equal to 2.5 g MJ^{-1} (PAR) for tomato grown in greenhouse (De Koning, 1993). The RUE is equal to 1.05 g dry weight MJ^{-1} m^{-2} (total radiation) for tomato growing in open field (Scholberg *et al*., 2000). According to Cockshull *et al.* (1992), the tomato fruit yield is in direct proportion to the accumulated solar radiation and 2.01 kg of fresh fruit weight are produced per 100 MJ of radiation incident on the crop. De Koning (1989a) found similar values, reporting radiation use efficiency equal to 2.07 kg of tomato fruit per 100 MJ of incident radiation. The theoretical RUE is 1.0 g dry mass MJ^{-1} of global radiation, which equals to 3.1 g dry mass MJ^{-1} of PAR inside a greenhouse (Challa and Bakker, 1998). In addition, values of 2.37 and 2.5 g dry mass MJ^{-1} of PAR in greenhouse were reported by Heuvelink (1995) and Sandri *et al.* (2003). The last authors reported that when tomato plants were grown at two irradiance levels (12.4 MJ m^{-2} day^{-1} and 5.0 MJ m^{-2} day^{-1}) the number of fruits per square meter did not differ significantly between treatments. However the dry matter from the last harvest of unshaded and shaded plants, differed significantly being 975 g m^{-2} and 762 g m^{-2} for total dry mass, 550 g m^{-2} and 420 g m^{-2} g for fruit dry mass, and 425 g m^{-2} and 343 g m^{-2} for vegetative organ dry mass, respectively.

The dry matter partitioning is not largely impacted by PPFD but it affects the total available assimilates for distribution. Cockshull *et al.* (1992) grew tomato in low shaded (6.4% light reduction) and highly shaded environments (23.4% light reduction) compared to the control. They found that the reduction in fruit fresh weight was 7.5% and 19.9%, respectively.

The total above ground biomass was reduced by 6.2% and 16.5% respectively. They also reported that over 14 weeks of harvest the dry weight accumulation was in direct proportion to the incident PPFD and regardless of the treatment 2.01 kg of fresh weight of fruit was harvested per 100 MJ received. The yield of tomato fruits depends on the number and the weight of the fruits. Cockshull *et al.* (1992) reported that fruit number per truss was positively correlated with the received radiation and a stronger effect was observed when less than 1.5 MJ m^{-2} day^{-1} was received at the time of anthesis of the first truss. Indeed, it has been repeatedly reported that the major influence of irradiance on tomato fruit yield is through its effects on the number of fruits that reach a marketable size. This effect is basically due to a high proportion of fruit abortion when the sink/source ratio is increased if low light integrals are accumulated at the time of flower initiation. Papadopulos and Ormrod (1990) reported that the plant spacing affected the percentage of tomato fruit set more markedly in spring than on autumn. For instance, they found that plant spacing of 60, 45 and 23 cm in autumn resulted in fruits sets of 62, 64, and 46%, respectively; whereas the same plant spacings in the spring led to fruit sets of 58%, 52%, and 13%. Heuvelink (1995) reported that the plant density had no direct effect on biomass allocated to the fruits, but the effects were indirect because it changed the fruit number (sink capacity) and that finally resulted in differences in biomass allocated to the fruits. Pearce *et al*. (1993) found that the rate of fruit growth was maintained during at least the first 20 hours after a tomato plant was placed on darkness. This suggests that current photosynthesis does not limit the rate of fruit expansion.

Light and carbon dioxide affect the yield pattern in tomato (Adams *et al*., 2001a; Adams and Valdez 2002). These authors found that when light levels were increased for a short time, there was no immediate effect on the yield. Yields subsequently increased, particularly four to

six weeks after the treatment started. This increase was mainly due to an increase in mean fruit size. Similarly, decreasing CO_2 concentration at weeks 24 to 26 caused depressed yields from weeks 28 to 31. Light levels and CO_2 concentrations affect photosynthesis and consequently the amount of assimilates available. Changes in the amount of available assimilate greatly affect fruits that are growing rapidly at that time. Newly set or nearly mature fruits will not be affected as much because their growth rates are low. Fruit set can be affected by the availability of assimilates and the fruit load on the plant.

Individual fruit growth: The cumulative growth pattern of tomato fruit is sigmoidal and follows three phases (Ho and Hewitt, 1986). According to Wang *et al*. (1993) there is an initial slow growing period from approximately 0 to 10 days after anthesis (DAA), then a tomato fruit accumulates most of its dry matter from 10 to 40 DAA. Subsequently, about 10 days after the first break of color the importation of carbohydrates ceases totally (Ho and Hewitt, 1986). Finally, there is a maturation period characterized by biochemical changes that leads to the fruit maturation. The fruit size is primarily determined by the cultivar. The fruit size also depends on its position on the truss, the competition for assimilates with other sinks and the water availability. The competition for assimilates depends on the number of fruits set on each truss, the number of plants per square meter, and the duration of fruit growth. Bailey and Hunter (1988) and Cockshull *et al.* (1992) reported that under shade the proportion of tomato fruits with small size increased. They attributed this decrease in fruit size to a lower assimilate supply in plants growing under shade which was proportionally reduced more than the reduction in fruit number under the same shade condition. Cockshull and Ho (1995) found that tomato plants grown at higher density produced more fruits per square meter. They attributed these results to a higher LAI for radiation interception in plants grown at high density compared with low density.

The overall weight of marketable fruit produced per plant however, fell from 19.7 kg at low density to 15.1 kg at high density. Papadopoulos and Omrod (1990) found a linear decrease in fruit weight (g fruit^{-1}) when increasing the plant density. Rates of fruit growth are found in the literature. Bertin (1993) for instance, measured a maximum rate of 1.04 g dry matter day^{-1} for a beefsteak cultivar, a very high value compared with other published data. Heuvelink and Marcelis in 1989 measured a rate of 0.2 g dry matter day^{-1} whereas values of 0.27 g dry matter day^{-1} and 0.37 g dry matter day^{-1} were published by Jones *et al.* (1991) and Ho *et al*. (1983), respectively. In agreement with the last authors, Aikman (1996) showed that a tomato fruit that takes 54 days from anthesis to maturity reached the maximum growth rate at day 23 and that rate was equal to 0.34 g dry matter day^{-1}.

Bertin *et al*. (1998a) studied the effects of cultivar, fruit position and seed content on the variability of the fruit weight in tomato under low and high competition for assimilates (one fruit and seven fruits per truss). They concluded that the variability in the potential fruit weight was mainly related to the cultivar and the fruit position on the truss. On average (of the first 15 trusses) the potential weight of the first fruit was 234 g, 283 g and 391 g for long life, round, and beefsteak cultivars, respectively. Likewise, the final weight of the fifth fruit was 219 g, 226 g, and 315 g respectively, that is 6 %, 20 %, and 19 % lower than for the first fruit. Increasing the number of sinks caused the weight of the first and fifth fruit to decrease at maturity regardless of the cultivar. Current tomato yield-predicting models do not take into account competition among sinks under low assimilate supply; this oversight could lead to prediction errors (Bertin *et al.* 1998). The reduction in fruit weight was not correlated with the truss position along the stem, but varied from 0 to 75 % among the first 15 trusses. Under competitive conditions, distal fruits were more affected by competition than proximal fruits in all cultivars. According to the authors, the

greater ability of proximal fruits to compete for assimilates under limited supply results from a faster accumulation of dry matter during the 25 days after anthesis due to the higher capacity to receive the phloem mobile assimilates in comparison with distal fruits. Bohner and Bangerth (1988) observed that the difference in cell number at anthesis could be responsible for fruit size at maturity. Bangerth and Ho (1984) showed that distal fruits before anthesis contain 18 % fewer ovules than proximal fruits and this may be a reason for the higher sink strength of proximal fruits. Regarding the relation between number of seeds and fruit weight they found that even when there was a correlation, this was not stable among cultivars and treatments.

Temperature

Although tomatoes are grown in many parts of world in open field and greenhouse, it is rather a subtropical specie because is subject to chilling injury when it is exposed to low temperatures above freezing for prolonged time. Tomato has been reported as responding positively to thermoperiodicity (Went, 1945). In addition, several authors have demonstrated the capacity of tomato plants to integrate temperature (Calvert, 1957; Hurd and Graves, 1984; De Koning, 1990). This means, for example, that a temperature regimen of 20/24°C (night/day) can be considered similar to a constant temperature of 22°C. De Koning (1990) demonstrated that tomato plants can integrate temperature over several days, and under large temperature amplitudes. This information however needs to be carefully interpreted because although different temperatures may have the same integral and have little effect on predictions of accumulated yield, this may not be true in analyzing the fluctuations of yield on weekly bases in which case the daily variations in temperature should be considered (Adams and Valdes, 2002). Moreover, temperature compensation is not possible for those processes with a strong interaction between temperature and some other environmental factor. The temperature has a large influence on growth and yield of the tomato crop and it is the major driving force of all the

development phases. According to Charles and Harris (1972) and Aung (1978), the optimum temperature for the tomato crop depends on the developmental state, cultivar and the organ being considered. Jones (1999) suggested some optimum ranges for tomato plant growth: air temperature 18-29°C, rooting temperature 18-24°C, and canopy temperature 20-23°C. Challa *et al*. (1995) gave the following ranges: germination 25/25°C (day/night) and after transplanting 22/17°C (day/night).

Plant development: The developmental processes such as flowering, number of leaves and fruit set have a strong impact on tomato yield (Heuvelink, 2005). To predict the plant development as a function of temperature, Monteith (1977) introduced the concept of thermal time which accumulation is given by the summation of temperatures above a threshold called base temperature (Ferreira *et al*., 1997). The base temperature used for tomato is inconsistent among authors and values of 4°C, 6°C, 7°C, 8°C, and 10°C have been reported (Warnock and Isaacs, 1969; Folker, 1979; Calado and Portas 1987; Scholberg *et al.*, 1997). Warnock (1973) for example, in Davis California (USA) used a base temperature of 6°C to calculate the degree days accumulated for tomato from seeding to emergence, anthesis, fruits of 2.54 cm in diameter, breaker fruit, and ripe fruit. The inconsistencies in the base temperature values may have several explanations but one possible reason is that the base temperature is not identical for all the life phases of the plant, therefore responses to temperature during the seedling phase, for example, may be different from responses during fruit setting or fruit ripening. However, one common base temperature is often considered for all stages of the crop. Another cause is reflected in the study published by Calado and Portas (1987). They worked at three locations during three consecutive years in Portugal and on different sowing dates. Their results, using the degree day approach by the intercept method, showed that the calculated base temperature for the same

tomato cultivar from anthesis to harvest was equal to 6°C, 8°C and 10°C for the three locations, respectively, where the base temperature increased from areas with a warm early spring to cooler ones. The hypothesis in crop modeling is that cardinal temperatures for a given specie and cultivar should hold constant across weather and sites. The failure to do so, is evidence of incorrect cardinal temperatures and temperature response equations. Another source that makes difficult the interpretation of published data is the methodology used to derive the cardinal temperatures. The most common method is the intercept method but the methodologies used are not always clearly established in the papers. Additionally, the method used to calculate the accumulated degree-days for each phase may be different among authors. For instance, most models use the daily average temperature minus the base. CROPGRO, however, uses hourly temperature, which is obtained from the maximum and minimum temperature data plus a decay function at night that predicts the hourly temperature accurately. The importance of these different approaches is that under the first approach even when linearity is assumed, this in reality may be not true and during a period of time the temperatures could be higher than temperatures at which a linear response is assumed and therefore the results may be biased. Another aspect to be considered is the type of function that the model uses to account for the temperature dependence of processes. To account for the dependence on temperature on several processes, the CROPGRO-tomato model uses a four point function represented by four cardinal temperatures: base temperature (T_b, the temperature below which the rate of the process is zero), optimum one ($Topt_1$ or temperature at which the rate reaches the maximum), optimum two ($Topt_2$, highest temperature at which the rate of the process is still at it maximum) and maximum (Tmax or temperature above which the rate is zero). Therefore, CROPGRO allows a punishment or deceleration of the process when temperature is beyond $Topt_2$ accounting in this way for heat

stress that delays the processes. Other models by contrast, only consider no increase in rate beyond the optimum temperature but there is no punishment by high temperature. The shape among this four point function in CROPGRO depends on the process. It is linear for development rate but may have different shapes for other processes (Boote and Scholberg, 2006). The default (V4.0) version of CROPGRO uses the same values of cardinal temperatures for the three phenological phases (vegetative, early reproductive and late reproductive phases) and those values are 10ºC, 28ºC and 55ºC for base, optimum (both $Topt_1$ and $Topt_2$) and Tmax, respectively. Just as for basal temperature, the maximal temperatures for tomato specie also vary according to authors and values of 48ºC (De Koning, 1994) and 50 ºC (Scholberg *et al.*, 1997) have been published. In addition, the maximal temperature is a value rarely found in literature.

Early vegetative and reproductive phases: According to Van der Ploeg and Heuvelink (2005), the optimum temperature for early vegetative growth of tomato plants is 25ºC. Tomato vegetative development can be thought as the leaf rate appearance and it is also related to the truss appearance rate since the specie is a sympodio with approximately one inflorescence every three leaves (Heuvelink, 2005). De Koning (1994) showed a linear increase of leaf appearance rate with increase of average air temperature, increasing from 0.2 leaf d^{-1} at 12ºC to a maximum of 0.5 leaf d^{-1} at 28°C and decreasing thereafter until reaching zero at 48 ºC. This author found that the relationship between temperature and leaf unfolding is linear in the range of 17 ºC to 23 ºC and 2.5, 3, and 3.5 leaves were unfolded each week at 17 ºC, 20ºC, and 23ºC respectively. According to Adams *et al*. (2001b), vegetative development in tomato has an optimum one ($Topt_1$) equal to 22 ºC and an optimum two ($Topt_2$) equal to 26 ºC. The base temperature for this phase according to their calculation is 7 ºC. They did not mention maximum (Tmax) values but as proposed by De Koning this value seems to be equal to 48 ºC. A linear relation between

flowering and air temperature has been observed by Abreu and Meneses (2000). Truss appearance rate increased linearly with a rate of 0.11 to 0.17 truss day^{-1} when average temperature was raised from 17 to 23 ºC (De Koning, 1994). According to De Koning (1993), the number of truss per week is enhanced by temperature with 0.05 truss $week^{-1}$ °C. Similarly Heuvelink (2005) found that in the range of 18°C to 23°C the truss appearance rate enhancement is 0.001 truss day^{-1} °C. The cardinal temperatures for the early reproductive phase or progression to anthesis according to Adams *et al.* (2001b) showed values similar to vegetative development having a base temperature equal to 7.2 ºC. In addition, they gave no data for maximum temperatures. Because this data is not available from other sources the same Tmax as used for vegetative development could be assumed. Therefore 7.2 ºC, 22 ºC, 28 ºC and 48 ºC for T_b, $Topt_1$, $Topt_2$ and Tmax respectively seems to be reliable to use as cardinal temperatures for early reproductive development.

Stem growth: The response of internode length growth to temperature, according to Langton and Cockshull (1997) followed a very marked linear trend ($p < 0.001$). They exposed tomato plants growing in cabinets to a factorial of 24 combinations of day (DT) and night (NT) temperatures ranging from 12 to 32ºC. Their experimental data for tomato growing over a 10 day period at 16, 20, 24, and 28ºC average NT and DT air temperatures, showed that the corresponding lengths reached by the internodes were 12, 18, 27 and 30 mm, respectively. Their experiments showed increased extension growth with increase in DT, and indicated that the optimum DT for extension growth is close to 28ºC.Similar, but less marked linear growth ($P < 0.05$) was shown for NT, with the optimum NT for extension growth being around 24ºC. The DT X NT temperature interaction was not significant. The stem growth is not directly used as an indicator of development in most models, however because the response to temperature is clearly

linear simulating more precisely the stem growth could be a path for differentiating the growth of determinate versus indeterminate cultivars.

Effect of temperature on NLPI: Dieleman and Heuvelink (1992) reviewed the factors affecting the number of leaves preceding the first inflorescence (NLPI) in the tomato plants. This factor is very important in tomato development because it determines the earliness of the crop and the transition from vegetative to generative growth. They stated that a lower temperature either in day or night during the sensitive period of tomato seedling growth causes a smaller NLPI independent of the cultivar or the tomato plant type. However the temperature does not affect NLPI if the light intensity is high. At low light intensity and high temperature, the NLPI increases. The effect of temperature on NLPI depends on the mean diurnal temperature while the root temperature has no effect within an ample range (12-35ºC). In addition, the authors pointed that tomato seeds do not respond to vernalization and therefore the temperature effect on NLPI is on the plant not on seeds. In brief, light and temperature effects on NLPI interact on tomato in such a way that higher light intensity decreases NLPI and higher temperature and low light increase it. This interaction is explained by the nutrient diversion theory proposed by Sachs and Hackett (1969) which has not been refuted until now. According to this theory a certain amount of photoassimilates need to be accumulated in the apex before tomato flower initiation takes place. Thus at low light conditions during the sensitive phase not enough assimilates are accumulated to switch from vegetative to reproductive growth. This is enhanced in high temperature because vegetative organs grow faster consuming the few assimilates available, and a high respiration rate at high temperature also consumes more assimilates. In high light intensity conditions, the effect of temperature is less marked because enough photoassimilates are produced. An elegant integration of that theory was recently published by Uzun (2006) who

performed a multiple regression analysis of the effects of temperature and light integral on the NLPI. His results confirmed the Sachs and Hackett's theory, the NLPI declined linearly with temperature and particularly at the lowest daily mean light integral. Because this role in determining the switch from vegetative to reproductive growth and also the earliness of the crop, the concept of NLPI could be very useful if it were incorporated into tomato models which until now simulate this transition only through the thermal time and allocation rules. Since NLPI is a function of light and temperature, both variables could be used to simulate NLPI. A caution note should be made; however, according to the Uzun studies this response to light-temperature interaction is not linear and therefore normalizing the equation for describing it may be difficult.

Fruit set and pollination: The temperature range for fruit setting in tomato is narrow and the night temperature is critical. The optimal range reported for fruit setting in tomato is 15 to 20ºC (Went, 1945), and 18 to 20ºC (De Koning, 1994). Fruit set is also low when the average maximal day temperature is above 32ºC and the average minimal night temperature is above 21ºC (Moore *et al*., 1952; Benedictos and Yavari, 2000). These last authors did not find cultivar differences in tomato with respect to flower abortion at high temperatures (37/21ºC day/night). Tomato fertility is affected by high temperature and this has a direct effect on yield through the number of fruits that are set on the plant. The simulation of this effect by tomato models has been poor in general. The CROPGRO-tomato species files includes a function that modifies partitioning limit (XFRT) to reproductive if temperature is too hot (reduced above 28°C and falling to zero at 33°C) and this function is a substitute for elevated temperature effects on fertility (Boote and Scholberg, 2006). For fruit pollination, the value for ceiling or failure temperature is critical because the fertility of tomato flowers is compromised at high temperature. The same values as proposed by Adams *et al*. (2001b) for progression to anthesis appear to be valid for fruit addition and

pollination except for ceiling temperature. According to Moore *et al.* (1952) and Benedictos and Yavari (2000) above 32 ºC is the failure day temperature for fruit setting and pollination while above 21 ºC is the night failure temperature. According to Heuvelink (2005) the range of flower fertilization in tomatoes is reduced at temperatures outside of the range 5 ºC to 37 ºC. The growth rate of pollen is increased between 10 ºC to 35 ºC but is reduced outside this range. According Atherton and Harris (1986), the failure temperature for fruit pollination is 40 ºC and the most critical stage appears to be meiosis, which occurs about 9 days before anthesis. The optimal temperature for pollination according to those authors is between 17 to 24 ºC. For base temperature, a value of 5 ºC was proposed and as a consequence, from Atherton and Harris the cardinal temperature for pollination seems to be: 5ºC, 17 ºC, 24 ºC and 40 ºC for $Topt_1$, $Topt_2$, and Tmax respectively. Since the Adams's *et al.* experiments were carried out in controlled temperature environments, it seems reasonable to adopt their values for modeling purposes and because of the strong effect of high temperatures on fruit setting to use a rather conservative value for ceiling temperature. As a consequence for fruit setting and pollination, reliable cardinal temperature values appears to be 7.2 ºC, 22 ºC, 26 ºC and 32 ºC for base, $Topt_1$, $Topt_2$, and T_{max} respectively.

Late reproductive phase: Assuming that the fruit growth period can be described by relating linearly its reciprocal to temperature, a critical temperature summation needs to be reached in order for fruits achieve maturity (Heuvelink, 2005). For this late reproductive phase (fruit development rate and progression to maturity), Adams *et al.* (2001b) found values of 5.7 ºC for base and 22 ºC for Topt1. De Koning (1994) proposed 4 ºC for base temperature, around 21 ºC for optimum and presented no data for $Topt_2$ and ceiling. Aikman (1996) proposed that the time from anthesis to maturity for tomato is 806 degree days using a base temperature equal to

4.75 ºC. Using the 4ºC of De Koning (1994) this time is 940 degree days while Scholberg *et al.* (1997), calculated 722 degree days using a base temperature equal to 10 ºC.

Fruit growth rate: Temperature is the climatic factor that most affects the fruit rate growth in tomato (Walker and Ho, 1977; Pearce *et al.*, 1993). Hurd and Graves (1984) suggested a Q_{10} value equal to 1.7 for tomato fruit growth and equal to 2 for fruit maturation (Hurd and Graves, 1984). For fruit growth rate (dry matter and water accumulation) Rylsky (1979) found an optimum equal to 26 ºC while Adams *et al.* (2001a) found a regimen of 25/25 ºC (day/night) to be optimum for fruit growth. Ho *et al.* (1983) found that the maximal rate of dry matter accumulation in tomato fruit at 19.3°C occurs around day 23 after anthesis (335 degree days over a base temperature equal to 4.75°C). Unfortunately, no data were reported for ceiling temperatures. De Koning (1994) proposed 10 ºC for base temperature but no data for ceiling. The ceiling temperature on the fruit growth rate seems more complicated to obtain since the water relationships in the system may influence the effect of high temperature on the fruit growth rate. Therefore, quality data for this parameter requires that both temperature and water should be controlled precisely. According to De Koning (2000), tomato fruit growth rate is relatively independent of temperature; however temperature appears to be the principal factor determining the duration of the tomato fruit growth period. His results showed this period to be 73 days at 17°C and 42 days when temperature increased to 26°C. Similar results were found by Rylsky (1979). In addition, Verkerk (1955) found that the time interval from anthesis to harvest was equal to 90 days at 13°C, 53 days at 19°C, and 40 days at 26 °C. In his experiment, De Koning divided the growth period in five states, and found different responses to temperature depending the fruit age. High temperature shortened the growth period in two phases, first at the young developmental state; the middle phase was insensitive to temperature, and again close to maturity

when temperature had a great impact on days to harvest. Adams *et al.* (2001) and Adams and Valdes (2002) found that when tomato plants were grown at 14, 18, 22 and 26°C, fruits ripened after 95, 65, 46 and 42 days, respectively, and the maximum fruit growth rate was achieved at 25/25°C. According to their results, fruits were more sensitive to elevated temperature in their later stages of maturation. In addition, their results showed a decline in days to harvest of 8.7 to 11.2 days when temperatures were increased by 7°C for a 3 week period above a value of 18°C. In summary, taking both processes together (fruit development and maturation), cardinal temperatures values according to these authors seems to be 5.7°C, 26°C, 28°C and 48°C for base, $Topt_1$, $Topt_2$, and Tmax respectively. Maximum temperature is not reported and therefore until other data is available, the same values as used for vegetative growth will be assumed.

Yield: The fresh weight of individual tomato fruits is strongly related to the number of locules present. Sawheney (1983), and Sawhney and Polowick (1984), studied the influence of the temperature on the size and locule number of tomato fruits. The study was conducted in temperature-controlled chambers with three thermal regimens: low (LRT) 18/15 ºC (day /night), intermediate (IRT) 23/18 ºC (day /night) and high (HRT) 28/23 ºC (day /night). The fresh weight, fruit diameter and locule number were significantly different under the three regimens. On average the fresh weight was 133 g, 96 g, and 73 g for low, intermediate and high temperature regimens respectively. The fruit diameter was equal to 6.99 cm, 6.05 cm and 5.42 cm, for the LRT, IRT and HRT treatments. The locule number was equal to 7.4, 8.5 and 6.99 (average). Houghtaling (1935) reported a correlation coefficient equal to 0.87 between the ovary size and the fruit size in tomato. Similarly, Young and McArthur (1947) reported that the gene lc which controls the number of locules in tomato fruits is correlated with the fruit size. Gibberellin application on flowers produced a similar effect as low temperature and produced a larger ovary

and a greater locule number in tomato fruits which resulted in bigger fruits. Overall, most of reports support that cool temperature increases fruit size (Went, 1957; Charles and Harris 1972; Sawheney, 1983). Rylsky (1979) reported that at even lower temperature the size of the fruits is reduced because of parthenocarpy. Sawhney and Polowick (1984), observed that less pollen was produced at very low and high temperature and more pollen at intermediate values. However, because all flowers were pollinated by hand the effects of a poor pollination were not studied.

Temperature often has strong influences on the demand for assimilates (sink strength) by the growing organs and therefore on the biomass allocation. In cucumber fruits, for example, the sink strength of individual fruits increases at increasing temperature, resulting in an increase of dry matter allocation to the fruits (Marcelis, 1992). In tomato, De Koning (1989), found similar results. However, he reported that further increase in temperature also reduced the number of fruits in such a way that the biomass allocation to all the fruits was not altered. Heuvelink (1995) found in a spring experiment that 56 to 60 % of cumulative dry matter was distributed to fruits, 28 -33% to leaves and 12-13 % to stems. On the other hand, late in autumn, when temperature decreased, the same author found only 35-38 % of dry matter was distributed to fruits, 44-45 % to leaves and 18-21 % to stem. However, due to lower radiation late in autumn that produced a poor fruit set, it is difficult separate the effects of light and temperature on allocation.

Bertin *et a*l. (2003) established that when the temperature is increased the tomato fruit growth rate increases; however she pointed out that the size and final mass of the fruit could be unchanged because the increased growth rate is compensated by a shorter growth period. The effect of temperature on tomato yield according to Adams and Valdes (2002) is correlated to both the earliness of the production and the yield fluctuations on weekly bases. Thus high temperatures during ripening phase results in a flush of ripe fruits. However, rapid fruit ripening

results in a decrease of the number of younger fruits approaching maturity on the plant, which then reduces yield in subsequent weeks. As a consequence, those authors proposed using temperature as driving variable to simulate the harvest dynamics of tomato.

Water

Fruit growth: Under non stress conditions, tomato fruit growth follows a sigmoid pattern that results from cell division during about the first two weeks after anthesis, and thereafter increase in volume (cell expansion) until the fruit reaches its final size (Coombe, 1976; Gillaspy *et al*., 1993, Monselise, 1978). The last process depends on the inflow of water which is linked to the carbon movement into the fruit. As a result, the growth of tomato fruit depends largely on the rate of water accumulation (Li *et al*., 1989). According to Ho *et al.* (1987), a large amount of water with assimilates is transported in the phloem sap to the fruit. Consequently, for modeling tomato fruit growth, the water relationships need to be understood. Tomato models in general simulate the fruit growth as a function of dry matter accumulation rate and the growth in fresh mass is generally ignored or deduced empirically from the dry matter accumulation. Lee *et al*. (1989) and Johnson *et al.* (1992) showed that the water flow into tomato fruits depends on the water potential difference between the plant and the fruit and consequently it controls the expansive growth of tomato fruit via phloem. Because transpiration from tomato fruits is negligible with respect to the whole plant (Johnson *et al.*, 1992), the water movement in the plant can be analyzed considering the water flow to leaves as only transpiration and water flow to fruits as only growth (Ya Ling *et al*., 2004). Ninety percent of water and dry matter entering the tomato fruit is via phloem, and water import via xylem ceases after the maximal growth of the fruit has been reached (Ethret and Ho, 1986; Ho *et al.*, 1987). Johnson *et al*. (1992) found a strong correlation between the fruit-stem water potential gradient and changes in fruit diameter. They showed that for tomato plants grown in high radiation, a threshold value between -1.1 to

-1.3 Mpa of stem water potential stopped the fruit growth presumably because the pressure gradient was too low to drive water flow into the fruit. These results are in agreement with data presented by Guichard *et al*. (1999) who found that high vapor pressure deficit (VPD) conditions reduced the fresh yield of tomato fruits mainly by its effect on water rather than dry matter influx, which was not affected. The fruit water potential (-0.4 Mpa) was not sensitive to VPD whereas the stem-fruit water potential gradient was reduced under high VPD conditions. On the contrary, low VPD increased the difference of water potential between fruit and stem maintaining the stem water potential around -0.28 Mpa and allowing fruit growth. Recent investigations published by Ya Ling *et al.* (2004) confirmed that the apoplastic stem-fruit water potential gradient seems to be a good indicator of both fruit growth rate and fruit weight. Considering that under adequate root water supply the fruit osmotic potential varies little, it is valid to propose that stem water potential will establish the gradient between fruit and stem. Therefore, only stem water potential could be considered in fruit growth prediction. Kawabata *et al.* (2005) studied the role of transpiration from tomato fruits in phloem transport and fruit growth. Their results showed that transpiration does not serve as a limiting step of carbohydrate transport to tomato fruits. Furthermore, although salinity effects will not be considered here, this issue has been well documented (Ethret and Ho, 1986; and Cuartero and Fernandez Munoz 1999; Mitchell *et al*., 1991). All these authors reported that salt stress influences both dry matter accumulation and water import into the fruits by effects on osmotic potential, maintaining dry matter accumulation but decreasing fruit fresh weight because less water is transported in xylem to the fruit and consequently the size is reduced.

Photosynthesis: The decrease in net photosynthesis in plants induced by water stress has been often reported. Mild stress may decrease photosynthesis by decreasing CO_2 diffusion due to

stomata closure and under severe stress biochemical reactions may be affected as well (Gimenez *et al.,* 1992; Lawlor, 1995). Castrillo *et al*. (2001) studied the effects of mild and severe water stress on tomato Rubisco activity, stomata conductance and leaf protein content. They found that a reduction in soil water potential (Ψ_w) produced a decrease in leaf Ψ_w. During water stress tomato leaf Ψ_w decreased gradually reaching a minimum -2.50 MPa on the 14th day and it had the lowest values until the end of the stress. The stomata conductance showed a gradual decrease during the stress starting to decrease at -0.7 MPa. The Rubisco activity in water stressed plants was stable at beginning of the stress, then began to decrease at a leaf Ψ_w of -1.70 MPa and reached the lower value at Ψ_w of -2.50 MPa. The tomato leaf protein content showed fluctuations at beginning of the stress period, at a Ψ_w of -1.50 MPa it decreased and was lowest at a Ψ_w of -2.50 MPa. Rahman *et al*. (1999) found that the photosynthesis rate, transpiration rate, leaf water potential and water use efficiency were reduced in tomato plants under water stress as compared with well irrigated plants while the stomata resistance and the leaf temperature was increased and those responses were cultivar dependent. Especially important was the difference among drought sensitive and tolerant genotypes related to the capacity of recovering under re-watering. Thus, the tolerant cultivars recovered shortly after re-watering while the sensitive ones took a significantly longer time to reestablish photosynthesis and transpiration rates.

Yield: The effect of water stress on tomato fresh yield is dynamic and complex to analyze. Factors such as timing of osmotic adjustment, interactions with nutrient status, especially nitrogen and potassium, time of occurrence, magnitude and duration of the stress, effects of the stress on reproductive sink activity and growth component being considered affect the response. The reports of osmotic adjustment in tomato are not consistent. In some studies partial osmotic adjustment was reported (Alarcon *et al*., 1994; Torrecillas *et al*., 1995). In other studies however,

no osmotic adjustment was observed (Perez Alfonsea *et al*., 1993). One weakness of those reports as pointed by Alian *et al*. (2000) is that the period of stress imposed was likely too short to see clear osmotic adjustment response. The studies on water stress are focused on fruit size, which is largely a measure of the fresh weight (Berman and Dejong, 1996). Research on tomato suggested that water stress limits fleshy fruit water accumulation but does not affect carbon partitioning to the fruits (Ehret and Ho, 1986). Scholberg (1996) evaluated the effects of water supply on tomato fruit yield grown in field conditions. His experimental data showed that fresh fruit weight was more strongly affected by water stress than fruit dry weight and the decrease of yield under stress was attributed to smaller and fewer fruits as compared with the control. These results agree with Ehret and Ho (1986), Mitchell *et al*. (1991) and Van Ieperen *et al.* (2005) who showed that water stress during growth of tomato fruit reduced fruit size by 30%. In addition, Garcia *et al.* (2004) found that one important response of tomato plants to early season water stress was a significant reduction in the number of floral buds and there was a delay in the floral buds appearance. Wolf and Rudich (1988) studied the effects of water stress on the tomato dry weight accumulation and fruit growth. The rate of dry matter accumulation was found to be higher in early than in later setting fruits and was unaffected by the water regime. Water stress however, shortened the duration of fruit growth and accelerated the ripening. Under water stress more than 40 % of the final dry weight yield was contributed by the fruits set during the first week of flowering. On the other hand, many investigations have reported that irrigating at a rate of 120 or 140% of evapotranspirative demand has increased significantly the fresh weight yield in tomato crops (Ortega Farias, 2003).

Bussiers (1993, 1994) studied the potential dry matter and water import rates in the tomato fruit in relation to fruit size. He found that the fruit radius is an important fruit size parameter

controlled by changes in water and dry matter imported into the fruit. This is because both flows are the product of two factors: 1) fruit surface area, which is radii dependent and 2) dry matter and water import rate per unit of fruit surface area. His results suggested that is more appropriate to consider the strength of the sink as being proportional to the product of fruit surface area multiplied by sink activity. Based on that, he developed models of water and dry matter import rates in tomato fruits and predicted partitioning to fruit as a function of fruit surface area and proposed that this relation could be used in fruit size simulations. Those models, although well sustained from a biophysical point of view, are difficult to incorporate into mechanistic models developed for tomato which are photosynthesis based and the water inflow into individual fruits is ignored.

Nitrogen

The ionic forms of nitrogen (N) used by tomato plants are ammonium (NH_4^+) and nitrate (NO_3^-). Tomato plants grow better with NO_3^- sources. When NH_4^+ is the major N source, toxicity can occur resulting in yield reduction (Barker and Mills, 1980; Jones, 1999). This is especially true in reproductive stages when, under NH_4^+ excess, the incidence of blossom end rot (BER) increases dramatically (Pill and Lambeth, 1977; Pill *et al.*, 1978; Jones, 1999). In early vegetative growth, however, NH_4^+ may be beneficial because of faster utilization and therefore a faster crop growth early in the cycle. In addition, Hartman *et al.* (1986) reported that a high NH_4^+ nutrition increases the phosphorus (P) concentration of the plant but reduces potassium (K), calcium (Ca) and magnesium (Mg). In the fruit, the P increased and K decreased while Ca and Mg were not affected (Jones, 1999). According to Adams (1986) N is essential for plant growth, influencing fruit number and yield. However, excessive N will increase the percentage of unevenly ripened (blotchy) fruits (Grierson and Kader, 1986; Jones, 1999). During the crop cycle tomato can uptake 150 to 300 kg ha^{-1} of N, but the response to N is more pronounced in the

range of 0 to 100 kg ha^{-1} (Larouche *et al.,* 1989). During rapid growth N uptake rates may exceed 4.3 kg $ha^{-1}d^{-1}$ (Dumas, 1990; Rinaldi *et al.,* 2007). According to Warner *et al*. (2004), the N requirements of tomato are higher during the vegetative than reproductive growth and their results agree with Scholberg (1996) and Scholberg *et al.* (2000) who studied the effect of N stress on growth and yield of tomato growing in field conditions. The results showed that severe N stress reduced significantly LAI, biomass and fruit yield by 60 to 70 % as compared with well fertilized plants. In addition, the concentration of N in vegetative organs such as leaves and stems was reduced under N stress, while the fruits, on other hand, maintained a relatively stable N concentration. Under N stress the RUE (dry matter produced per unit light intercepted) was reduced by about 30 % and the authors related this reduction to a lower leaf N concentration which in turn affected the photosynthesis rate. The leaf photosynthesis rate also was reduced by 30 % compared to control plants although the leaf N concentration was dramatically reduced (40 to 15 mg g^{-1}). One of the reasons was that SLW increased under N stress, thus causing specific leaf nitrogen (SLN) to be considerably maintained despite large decrease in N concentration. Lawlor (2002) published a complete review about the relationship between photosynthesis and SLN. It is largely accepted that the leaf photosynthesis response to irradiance depends on the SLN (Evans, 1989). The maximum rate of photosynthesis (A_{max}) increases asymptotically to the leaf N content and this relationship is true either considering SLN per leaf area unit or per leaf weight unit (Grindlay, 1997). The maintenance of a relatively high SLN in plants under N stress concurs with the Scholberg *et al*. (2000) observations who found only 30 % of reduction in leaf photosynthesis rate of plants exposed to N stress as compared with the control treatment although the N concentration was dramatically reduced. The impact of N is frequently evaluated in leaf photosynthesis terms and the effect of N on building the source of assimilates, but

information about the fruit sink response to N limitations or the fruit growth rate is scarce. Huett (1986) and Huett and Dettman (1988, 1991) reported that increased yield of semi-determinate tomatoes in response to increasing N was associated with higher ratios of fruit dry matter to total plant dry matter. That means that in tomato crop where the fruits are the dominant sinks, apparently the N level influences the dry matter partitioning to the fruits. Hebbar *et al.* (2004) reported an average of 33 % of higher fruit yield in fertigated tomatoes especially related to N fertilization and drip irrigation method, they attributed this yield increment to a higher LAI, number of fruits, dry matter production and fertilizer use efficiency.

Partitioning of Assimilates Within a Tomato Plant

Partitioning of assimilates among plant organs is often described by the concepts of source and sink. Source is a plant part that exports more carbon than it imports, while sink is a plant part that imports more than it exports (Ho *et al.*, 1989). The ability of a sink to import assimilates is referred as sink strength. The sink strength can be quantified by the potential growth rate of a sink, i.e. the growth rate under conditions of non-limiting assimilate supply (Heuvelink and Marcelis, 1989). According to Farrar (1988), Ho (1988) and Marcelis (1992), the distribution of assimilates among sinks is primarily regulated by the sinks themselves. Tomato fruits are very strong sinks for carbohydrates (Ho, 1984; Wang *et al.*, 1993). In tomato crop the fruits are the most important sinks (De Koning, 1993), therefore it is expected that the dry matter distribution between vegetative and generative sinks is mainly regulated by the fruits. Under normal conditions, photosynthetic supply does not limit fruit growth in tomato because the source exceeds the sink demand (Khan and Sagar, 1969; Tanaka and Fuyita, 1974; Heuvelink and Buiskool, 1995). De Koning (1994) reported a source- sink ratio for tomato of 0.5 for indeterminate greenhouse grown cultivars which means a weak source limitation compared to other fruit crops. Hurd *et al.* (1979) and De Koning and De Ruiter (1991) observed that when the

number of fruits per tomato plant was increased, the fruit growth increased at the expense of vegetative growth. However, a balance in the source sink ratio needs to be reached for indeterminate greenhouse cultivars because if the source to sink ratio is too low (less leaf area and light interception) flower/fruit abortion may decrease the fruit yield (Bertin, 1995). Heuvelink (1997) published the results of experiments that were carried out in order to establish the relationship between the fruit load and the dry matter partitioning in tomato plants. He found that the dry matter distributed to the fruits can be described by a saturation type function of the number of fruits retained by the truss. According to this relationship the generative sink strength was proportional to the number of fruits (in a range of two to seven). The fraction partitioned to fruit was almost halved when fruit number was decreased from 7 to 2. The average sink strength of the vegetative sink (three leaves and the internodes between trusses) was 2.96 times the average sink strength of one fruit. Consistent with these results, the average dry matter partitioning to the fruit over time increased with the average fruit number on the plant during the time interval. The weight of individual fruits was increased when the number of fruit decreased but this diminution was less than proportional. At higher than seven fruits per truss the relationship was not more proportional. Indeed, De Koning (1994) observed a low potential fruit weight when the fruit number per truss was over seven. Heuvelink and Buiskool (1995) demonstrated that reducing the number of fruits per plant strongly diminished the biomass assignment to the fruits, whereas the total dry matter production was hardly affected. In addition, temperatures, in a range of 9 to 23 ºC, and irradiance in a range of 8 to 15 MJ m^{-2}, hardly influenced partitioning. The knowledge of the relations mentioned above is useful in simulation models. Heuvelink and Marcelis (1989), for instance, used a constant value of 3 g per day per plant for total vegetative sink strength. The simulated average sink strength of a fruit was 0.129 g

per day. Those values are consistent with the constant ratio value between vegetative unit and one fruit which, as was mentioned, is equal to 2.96. Thus in a tomato plant with 8 growing vegetative units (De Koning 1994), results in 2.96 *0.129*8≈ 3 g per day total plant vegetative sink strength as published in the experiments of Heuvelink and Marcelis. Regarding partitioning of dry matter to fruits average values between 54-60 % and maximum of 64 % and 67 % were reported by Heuvelink (1997) and Aikman (1989), respectively. Heuvelink (1995) found that in spring 56 to 60 % of cumulative dry matter was distributed to fruits, 28 -33% to the leaves and 12-13 % to the stems. However, in autumn only 35-38 % of dry matter was distributed to the fruits, 44-45 % to the leaves and 18-21 % to the stem. De Koning (1993) found a fruit partitioning equal to 72 % in commercial crops and over the whole season while Cockshull *et al.* (1992) estimated that the 69 % of the produced biomass was allocated to the fruits. The results of Aikman (1996) are close to those values since he reported that 67 % of the dry matter is allocated to fruits in tomato. He calculated that 1 mol of carbon assimilated as CO_2 would give about of 0.4 mol harvested in carbohydrate, about 12 g harvested biomass or 200 g harvested fresh weight. Lower values were found by Ehret and Ho (1986) and Scholberg *et al.* (2000) who reported that 58 % of total above dry matter produced by tomato crop was allocated to fruits. The fruit dry matter concentration may be influenced by the fruit number, the temperature and the duration of the growth season. The average fruit dry matter concentration was 5.6 % according to Ehret and Ho (1986). In agreement with this, values of 5.4-6 % were reported by Winsor and Adams (1987), 5.5 -6 % by De Koning (1993), 6 % by Aikman (1996), and 5 - 7.5 % by Davies and Hobson (1981).

It could be argued that the sink strength is strongly dependent on the developmental stage of the fruit as was demonstrated by De Koning in 1994 but the same author argued that when the

development is normal there is a correlation between the fruit number and the fruit age as well. Therefore, the relationship found between the fruit load and the dry matter partitioning to the fruits is still valid. However, it does not imply that always the number of fruits on a plant will determine the dry matter allocation to the fruits. Other aspects such as severe stress and competition between fruits within a truss are frequently mentioned as factors that may alter the biomass allocation to fruits (Aikman, 1996; Bertin, 2005).

According to Huevelink and Buiskool (1995), the influence of the sink demand on dry matter production per unit of intercepted radiation and probably on leaf photosynthetic rate in commercial tomato production can be ignored. Therefore and different from other crops in which feedback inhibition is reported, reducing fruit number (sink strength) in tomato plants apparently does not reduce the photosynthetic rate. They found that while the production of dry matter was not influenced by sink-source ratio (except in the extreme case of one fruit per truss), the distribution of dry matter between fruits and vegetative parts was greatly affected. Thus, of the same amount of dry matter produced, the partitioning was highly variable and a fraction of 0.3 to 0.6 was allocated to the fruits depending on the fruit number. Lack of influence of sink-source ratio on dry matter production in tomato plants was also supported by Ho (1992) who concluded that only in extreme cases (pruning all the fruits) a low sink demand will negatively influence the photosynthetic rate. According to Huevelink and Buiskool (1995) the source sink ratio did not affect the plant development and the number of visible leaves at the end of the experiment was the same for pruned and unpruned plants. However, the specific leaf area and the internode length decreased (heavier stems and thicker leaves) and the plant leaf area increased when the sink source ratio was reduced. The truss appearance rate and fruit growth period are hardly influenced by sink-source ratio (De Koning, 1994). While the plant leaf area is not affected by

competition for assimilates except under extreme conditions, the leaf mass per area (SLW) or the inverse the specific leaf area (SLA) show large fluctuations when the source sink activities are altered. Bertin and Gary (1998) showed that under artificial manipulation of the sink-source ratio through shading, CO_2 enrichment or fruit removal, the dry weight of the leaves and as a consequence, the SLW or SLA underwent large and rapid fluctuations. For example, a reduction in 60 % of photosynthetic active radiation (PAR) led to a 24 % decrease in SLW after 10 days. Carbon dioxide enrichment and fruit removal produced an increase in SLW of 45 and 15 % respectively on plants with two fruiting trusses, but hardly affected SLW of producing plants. They did not observed cultivar differences in these responses. Based on their results those authors proposed that the structural SLW varies between a maximum and a minimum according to the ratio of assimilate supply and the demand during leaf development. They also proposed that when a maximum SLW occurs, a storage pool of assimilates might have accumulated in leaves during periods of high supply and low demand. The concepts of SLW or SLA are very important in crop models because they are frequently used to predict leaf area expansion and consequently light interception based on the dry weight of the leaves. Reduction in sink number also induces variation of SLW in tomato leaves (Bertin and Gary, 1992). The variations can be related to changes in the level of starch and hexoses in tomato leaves (Shaw *et al*., 1986). According to Bertin and Gary (1998) the fluctuations in sugars and starch accounted for 29 % of the daily variation in SLW when the sink source ratio is manipulated; therefore they hypothesized that fluctuations in other components in leaves, besides sugars and starch, may be involved in the changes of SLW. In some models, the SLA is a constant or it varies in responses to climate or the season. In other models, the leaf area growth is mainly a function of the plant leaf age and temperature ignoring mass. Still there are models in which leaf expansion is

function mainly of temperature but water or nitrogen status is allowed to modify the potential growth. The source sinks interactions, however, as affecting the leaf weight normally has not been considered in crop models to describe fluctuations of SLA. This is a weakness and may affect the accuracy of the leaf growth predictions. Gary *et al*. (1995) proposed to simulate SLA as a function of leaf age and temperature but allowing structural SLA to vary between a minimum (full satisfaction of growth demand) and a maximum (minimum leaf thickness) (Gary *et al*. 1995; Heuvelink, 2005). This approach might be a path to improve the simulation of SLA fluctuations and therefore of the leaf expansion as well.

Temperature often has strong influences on the demand for assimilates (sink strength) by the growing organs and therefore on the biomass allocation. In cucumber fruits, for example, the sink strength of individual fruits increased at increasing temperature, resulting in an increased dry matter allocation to the fruits (Marcelis, 1992). Similar results were found by De Koning (1989) in tomato. However, they reported that the increase in temperature also reduced the number of fruits in such a way that the biomass allocation considering all the fruits together could be not altered.

There are several reports of the role of the irradiance on dry matter partitioning. Papadopoulos and Ormord (1990) for instance, found that the dry matter distribution to the tomato fruits increased with increased plant spacing and they argued that this effect can be attributed to an increase in the light interception per plant. Cockshull *et al.* (1992) found that a reduction in solar radiation by 23 % had no effect on the dry matter distribution to tomato fruits although the number of fruits was reduced. Yoshioka and Takahasi (1981) on other hand, fixed the fruit number and observed decreased assimilate allocation to the fruits when the irradiance increased. The distribution of assimilates in tomato plants is not affected by osmotic stress within

certain limits. The tomato specie is relatively tolerant to salinity. Ehret and Ho (1986), reported that salinity values up to 6 mS cm^{-1} did not affect the dry matter partitioning in tomato plants. Grange and Andrews (1993) established that there is close relationships between the rates of assimilate importation during the rapid growth phase and the final weight per fruit. The rate of assimilate importation is affected by temperature and under normal circumstances the increase of temperature increases the rate and in consequence the fruit weight. However, this is true if the assimilation and water supplies are not limited. Under water stress an increase in temperature likely will increases the canopy and fruit transpiration which will affect the fruit weight mainly because a reduction in its volume. The dry weight however, may be less affected because even when water stress reduces the phloem sap volume, the concentration of dry matter in fruit increases, therefore the rate of importation of assimilates remains relatively stable (Ho *et al*., 1987). Osmotic stress may have similar effect on the dry weight assimilation rates.

The potential strength of different sinks is related to the developmental stage of the plant. In addition, the potential strength of the fruits is related to the phyllotaxy of the plant and to hormonal regulation as well. In concern for hormonal regulation, Ho cited the reports of Kinet (1987) and Kinet *et al*. (1978, 1986) who established that the apparent role of the auxins on the fruit strength is related to the cell division activity in the ovary which is hormonally regulated. This theory is also the basis for the close and positive relationships frequently found between the weight of tomato fruits and the seed number since it has been argued that the capacity of seeds to produce auxins appears to stimulate the cell division in the ovary.

The duration of fruit growth from anthesis to maturity is not highly variable among cultivars being in the range of 40 to 65 days. Because there are huge variations in fruit size among cultivars, one can infer that the source of this variation is different rates of dry matter

accumulation among them. In fact, mutants of tomato plants with altered number of cells in the ovary of the fruit during pre-anthesis have demonstrated that the cell number is a good measure of the sink size and determines the strength of the fruit to attract assimilates thus affecting the final size of the fruits. In addition, even though the auxin production has been reported as the reason for good correlation between the number of seeds and the fruit weight, other authors suggested that this correlation is in fact related to the number of seeds which correlates with the number of ovules per se and this in turn determine the cell number in the ovary. However, parthenocarpic fruits that still reach a commercial size make difficult the last interpretation.

The photosynthesis of tomato fruits is negligible after reaching a diameter of 15 mm (Bertin *et al*, 2001). Therefore, the carbon balance of tomato fruits depends on the importation of assimilates from leaves. Sucrose is the main sugar transported (Walker and Ho, 1977); however, sucrose does not accumulate in fruits but it is converted in hexoses, which account for 75 % of the soluble solids in a ripe tomato fruit. According to Ho *et al*. (1983), during the first week after anthesis sugars and starch account for 10 % of the dry weight of the fruit. In a fruit of 3 weeks, 20 % of the dry matter is starch. After that, the sugar proportion increases until a steady value which ranges between 50 and 75 %. Even when a tomato fruit does not accumulate significant amount of starch except in the early development, Dinar and Stevens (1981) showed a positive relationship between the amount of soluble solids in a ripe fruit and the rate of starch accumulation during early green stages. This relationship has been explained as the starch assimilation in early cell enlargement provides an extra capacity to store imported sugars.

Genetic Traits Related to Tomato Yield

Fruit and yield characteristics of tomato plants are controlled by genetic and environmental factors (Scholberg, 1996). There are more varieties of tomato sold worldwide that any other vegetable (Foolad, 2007). However, selection for yield per se is not successful in general because

yield is a complex trait influenced by genetic and non genetic factors, and therefore, the heritability for yield is very low in most crops including tomato (Foolad, 2007). Consequently, the breeders normally bred for components of yield that contribute to it. In tomato, for example, targets for breeding have been: disease resistance (Bournival *et al*., 1990; Scott, 2003), tolerance to abiotic stresses (Vallejos, 1991; Foolad, 2005), earliness and fruit solid content (Fridman *et al.,* 2000; Georgelis *et al,* 2004) among others. According to Foolad (2007) the history for improved tomato fruit yield through different attributes has been very successful. For example, between 1920s and 1990s, fruit yield of processing tomato cultivars in the U.S increased from 10.1 to 72.4 tons ha^{-1} (Warren, 1998). On average, half of this increment is attributed to breeding and the other half to improvement in management practices (Duvick, 1986). In the fresh market cultivars, the University of Florida's breeding program has achieved increases in yield by breeding for heat tolerance for production under hot and humid conditions (Scott, 1997). Genetic studies have shown that most tomato traits of economic importance that distinguish cultivated tomatoes from their related wild species are due to quantitative trait loci (QTLs). Molecular mapping for instance has revealed the presence of several dozen QTLs associated with variations in tomato fruit size. For many tomato varieties, the differences in fruit size are established by the time of flowering and the size of the ovary becomes a good predictor of the final size of the fruit (Yeager, 1927; Grandillo *et al.,* 1999). Szymkowiak and Sussex (1992) showed that in tomato the meristem size and the number of carpels is determined by the number of cells in an internal layer of the shoot meristem and this layer determines the eventual sink strength of the developing fruits. A QTL of tomato called fw2.2 has been cloned and characterized and seems to make the largest contribution to size variation between the cultivated tomato genotypes and their small wild species relatives. The QTL *fw2.2* appears to determine the

difference in fruit weight and diameter (Liu *et al*., 2003). According to Frary *et al*. (2000) allelic differences at *fw2.2* increase fruit weight by 30 percent. Nesbitt *et al.* (2001) studied whether the change in tomato fruit size caused by *fw2.2* is associated to other phenotypic changes that indirectly affect fruit size. They concluded that the primary effect of *fw2.2* is on controlling fruit size although there are other secondary aspects associated, such as fruit number and photosynthate distribution. The number of QTLs reported as affecting tomato fruit fresh weight varies from 3 (Bernachi *et al.*, 1998) to more than 18 (Esehd and Zamir, 1995). Grandillo *et al.* (1999) estimated that a common set of 28 QTLs for fruit fresh weight can be identified for tomato that shows segregation in at least two independent studies. Zeng *et al*. (1990) suggested a similar number of QTLs affecting fruit fresh weight in tomato. In similar way diverse amount of QTLs affecting the shape of tomato fruits have been identified and the number varies from 2 to more than 16 QTLs. Moreover, a common set of 18 QTLs for fruit shape can be identified for tomato that shows segregation in at least two independent studies. The two major fruit shape QTLs, *fs2.1* and *fs8.1*, have been characterized and round shape is partially dominant over the more elongate shape (Grandillo *et al.*, 1996). On the other hand, several qualitative genes have been mapped in different chromosomes of tomato that exert effect on fruit size or the number of locules. For example the gene ovate reduces the fruit weight by half whereas the gene faciated increases the number of locules and seeds increasing the fruit weight by 60 % (MacArthur and Butler, 1938).

The potential use of “real” genetic parameters in models instead of the empirical ones has been frequently proposed as a possible tool to improve the physiological bases of mechanistic models. This task is technically very difficult in cases like tomato in which the main genes that define yield and quality traits are quantitative and therefore the inheritance patterns are normally

polygenic. Consequently, it is almost impossible to assume independency of characters for parameterization purposes. Still another approach for this goal could be to study the inheritance of other traits not directly involved in yield, but related to it. For example, the traits that define the earliness and the life cycle of the specie. Molecular techniques that allow cloning and characterizing QTLs are potentially valuable tools that can help in the future to obtain better results in this area but the link with modeling is still weak. In 2006, Thornley quoted *"Does the massive amount of data now being produced by genomics, proteomics and metabolomics change fundamentally the "modeling project"*? His short answer was no and nothing has changed because qualitatively the biology is the same. He cited Popper (1959) to say "*models still operate within the loop of hypothesis, analysis, synthesis, prediction, test against real data and back to hypothesis*". What could change with what Thornley called the "omics" data avalanche is that there is now an increased opportunity for relating predictions to properties defined at molecular level with all the possibilities that such knowledge may provide. According to Thornley, trying to construct models going from molecular level to the whole system in one bound is not viable but what is possible and really matters is to establish connections between the top and the bottom of the system, step by step, to all the intermediate levels of organ tissues, cell and sub cellular and when those connections are made, then the understanding and therefore the ability to simulate and intervene the systems will be maximized.

Tomato Models

Horticultural models were developed significantly in the eighties as consequence of the need for quantitative information tools to improve decision making to control greenhouse environments (Gary *et al.*, 1998). Gary's paper was a complete review describing the state of art of horticultural models. Other reviews about specific topics of horticultural models were written by Le Bot *et al.* (1998) who reviewed the modeling of mineral nutrition in horticultural crops,

Jones and Tardieu (1998) who focused their review on water relationships while Marcelis *et al.* (1998) reviewed the modeling of biomass production and yield of horticultural crops. After 10 years of those reviews, the topics pointed as still being in their infancy continue in that sate and models fail to consider, for example, the interaction between pests and diseases coupled directly to horticultural models, the use of real genetic parameters as commented above, the simulation of plant architecture and morphogenesis, the simulation of fresh matter production rather than only dry matter production and the modeling of quality traits among others.

Models for tomato have focused on the carbon balance that leads to predictions of fruit growth in dry mass. Some examples are TOMGRO (Jones *et al.*, 1991), CROPGRO-tomato (Scholberg *et al.*, 1997), HORTISIM (Gijzen *et al.*, 1998), TOMSIM (Heuvelink and Bertin, 1994), TOMPOUSSE (Gary *et al.*, 1997) SIMULTOM (Sauviller *et al.*, 2002).

In crop oriented process models, the biomass production is based on the carbon balance which depends on the gross photosynthesis of the canopy in turn closely related to light interception and therefore to the leaf area, leaf photosynthesis and the losses of carbon through respiration process. Leaf photosynthesis is modeled using different equations depending on the model, but independent of the function shape used, most of them follow a curve of saturation type where the main parameters are A_{max} (maximum photosynthetic rate) and the initial slope of the light use efficiency (Gary *et al.*, 1998). Scholberg *et al.* (2000) reported an A_{max} value for tomato equal to 1.36 mg CO_2 m^{-2} s^{-1} a higher value than values used by other authors such as Heuvelink (1995) who uses a value equal to 29.3 µmol CO_2 m^{-2} s^{-1} which is equivalent to 1.2 mg CO_2 m^{-2} s^{-1}.

Some models calculate the gross photosynthesis integrating it from leaf level to canopy level. The most simple, take the projected leaf area and just multiply it by the unit leaf

photosynthetic rate. All consider also the extinction coefficient of the light. In addition, some models calculate photosynthesis at leaf level using a Farquar's kinetics approach or at canopy level using a rectangular hyperbola function or an exponential curve. The light distribution for tomato canopy which grows in rows needs to take account of the distribution of direct and diffuses light, the light scattering and leaf angle. An example is the hedge row model (Boote and Pickering, 1994).

Jones and Tardieu (1998) reviewed the modeling of water relationships in horticultural crops. According to them, the task of simulating water relationships by the models was related to simulating the water requirements by the crops for transpiration purpose and soil evaporation. Therefore, models have been based on the water balance that considers water inputs (precipitation and irrigation) and water outputs (canopy transpiration, soil evaporation) and diverse losses such as runoff, deep percolation, etc. The evapotranspiration is mostly modeled using energy balance approaches such as the Penman- Monteith or Priestly-Taylor equations. The second aspect that has been included in some models is the influence of the plant water status on functions such as stomata aperture, organ growth in extension and assimilates fluxes. However, the tomato fruit is about 95 % water (Davies and Hobson, 1981), thus the water flux into the fruit is one of the key aspects in the fruit yield formation of this specie. The fundamentals to simulate water and assimilate movement through both phloem and xylem into the fruit were published by Guichard *et al*. (1999). A virtual model was published also by Genard and Lescurret (2005) for peach specie. In those models the xylem flux depends basically on the stem water potential while the phloem flux depends mainly on the dry matter concentration of the phloem sap. Recently published is a model for simulating carbon and water fluxes into individual fruits of tomato developed by Liu *et al.* (2007). The water efflux from tomato fruits

was modeled by Leonardi *et al.* (2000) as a function of radiation and the vapor pressure deficit (VPD). Bussieres (1994) on other hand, proposed that the tomato fruit transpiration is a small and constant proportion of the fruit mass. The last approach may be realistic considering that the transpiration of tomato fruit is actually limited due the resistance exerted by the epidermis. Even when a few advances have been published, the task of modeling the water and assimilate fluxes into individual fruits and then coupling it to a more integrated whole plant model is still in its infancy. However, this may be an unavoidable step in order to improve the fruit growth and quality simulation. On the other hand, the latest version of DSSAT (4.5), not yet officially released, has incorporated a routine for deriving the fresh weight of individual fruits from the carbon balance and then converting the fresh weight to fruit size. This routine appears to work reasonably well according to initial testing (Boote and Scholberg, 2006) but further validation with field data needs to be done. One issue in this derivation is how the model deals with water stress in view of the smaller impact of water stress on the carbon balance as compared to its impact on fresh production. Therefore, further functional modifications might be needed. As for carbon, mechanistic sub models have accounted for the mineral balance in the plant. However, only the nitrogen is generally considered explicitly and the process of uptake, canopy accumulation and redistribution of N according to partitioning rules and organ ageing are often simulated. With respect to the soil nitrogen, some models have incorporated modules for simulating organic matter and dynamics of both organic and mineral N in the soil. One example is CROPGRO-tomato model which allows the users to couple the simulation to specific models for soil organic matter budget such as modified CENTURY (Gijsman *et al.*, 2002).

In summary, the tomato fruit growth has been modeled based on the canopy dry matter production and subsequent accumulation into the fruit. The biomass production by the canopy is

photosynthesis driven. The integrated net photosynthesis normally on a daily basis is converted to biomass and it in turn is converted into accumulated dry matter according to established rules for partitioning and fruit growth. In addition, the biomass production is regulated by the efficiency of conversion of the intercepted radiation in dry matter. The water inflow into the fruit has been ignored at least until recent efforts particularly led by French researchers. Bussieres (1993) for example published a pioneering work simulating the rate of water importation into tomato fruits as dependent on the difference in water potential between the stem and the fruit. Previously Lee (1990) and Genard and Huget (1996) simulated the water uptake and transpiration of tomato fruit per area unit as a constant or a variable function, respectively. Regarding crop development, most tomato models are based on the fact that development depends mainly on the temperature and in the range of a tomato plant growing conditions this dependence is linear. Thus, most tomato models simulate the timing of organ appearance, development, and phase transitions as a function of the accumulated thermal time. Some models use simple equations that originally were formulated to describe the responses of enzymatic process to temperature and follow the classical bell shape curves. Other models are more elaborate; CROPGRO for instance, has four point functions that follow a rectangular or sinusoidal shape and where each point represents a cardinal temperature: base, optimal one, optimal two, and maximum (failure) temperatures. In addition, in some models the fruit number is an input. More realistic are those models such as CROPGRO that predict the phase transition from tomato flowering to fruit setting and then establish a fruit population based on a sequence of cohorts added after the anthesis date and which accounts for the accumulated thermal time and the assimilation carrying capacity. The growth of the tomato fruits depends on the amount of assimilates and water that is assigned to the fruit. The assimilates partitioned to the fruits depend,

in turn, on the capacity of the fruit to attract them (sink strength), and on the equilibrium between generative and vegetative sinks. In case of indeterminate cultivars growing in greenhouse the strength of the sink depends on the number and the age of the organs. In fact, the current models for tomato do not specifically discriminate between the more determinate cultivars and the sink-source relationships of cultivars such as those growing in open fields as compared with indeterminate cultivars grown in greenhouses. The simulation of the fluxes of dry matter and water into the fruits is not common in tomato models which simulate only the carbon influx and then use empirical relationships to convert the accumulated dry matter in fresh weight. The attempts to couple both fluxes and to mechanistically predict both dry and fresh fruit weight is slowly being studied. At present the theoretical models for tomato developed by Bussieres (1993, 1994,), Fishman and Genard (1998) and its recent adaptation for tomato by Liu *et al.* (2007) are good examples of those attempts. However, the number of parameters related primarily to the simulation of the resistance path to both fluxes as well as to the wall extensibility coefficients among other parameters may impose restrictions for practical applications of such models. Nevertheless, they seem to be a valuable tool for increasing the knowledge of the complex behavior of tomato fruit growth.

CHAPTER 3
UPDATING PARAMETERS IN CROPGRO AND TESTING THE MODEL FOR PREDICTING GROWTH AND DRY MATTER ACCUMULATION

Introduction

Calibration is an important task in the crop modeling process and it can follow different paths. Scholberg *et al*. (1997) adapted the CROPGRO-model for tomato simulation; however, no further improvements have been introduced. A sub model for predicting fresh weight and fruit size from the dry weight of the fruits will be presented in Chapter 5. This sub model starts with the carbon balance and therefore, biases in dry matter predictions can be propagated to fresh weight prediction, which in turn will also affect fruit size simulation. For this reason, the objective of the present chapter is to make a literature based adaptation of parameters of the CROPGRO-Tomato model related to the simulation of crop development, daily dry matter (DM) production, DM partitioning and DM accumulation in the crop from transplanting to harvest. The adaptations took advantage of new literature values for species parameters, especially cardinal temperatures that affect tomato phenology. Recent literature reviewed in Chapter 2 suggested that the cardinal temperatures that drive the phenology and plant processes are different from the values used by Scholberg *et al*. (1997) and that are still present in the current version of the tomato model. The new cardinal temperature values are considered to be reliable as they come from recent published data of experiments conducted in controlled-temperature environments. The second objective of this chapter is to calibrate the model using field data in response to these changes, and evaluate its capability for predicting growth and dry matter accumulation of the tomato crop through time.

Materials and Methods

Approach: A systematic approach for model improvement as proposed by Boote *et al*. (2002) was followed and can be summarized in three steps. First, an adaptation of the parameters

was performed based on data reported in the literature. The adapted species coefficients were cardinal temperatures for pre-anthesis, anthesis, and post-anthesis phases. Second life cycle phase durations and other parameters were calibrated against growth data from field experiments. Third, the quality of the model predictions was evaluated using statistics such as RMSE and the Willmott index as evaluation criteria. Calibration (second step) was performed according the following order:

A) Life cycle was adjusted with the new cardinal temperature by comparison against the phase durations observed during experiments carried out during the spring season in Gainesville Florida in 2006 and 2007 and attempts to predict the observed dates for the occurrence of first flowering, first fruit, and maturity. This was required because observed data for phenology were not available for most of the experiments, and therefore the hypothesis in this effort was that the life cycle duration of the 2006-2007 experiments should be reproduced since cultivars for fresh market grown in Florida are similar and no important differences in the phase duration among them have been reported. On the other hand, the simulated phase durations calibrated using Scholberg's field data and the default parameters showed differences as large as 18 days for time to flowering for the same cultivar, growing during the same season and at the same location. The weather records of those experiments do not explains these huge differences in time to flowering. As a consequence, we assumed that such discrepancies were attributed to the model using incorrect cardinal temperatures for the phenology of the specie. Because the phase duration for cultivars used in Florida for fresh market are similar if they are grown during the same season, we assumed that one standard cultivar can be created for tomato with no differences in genetic parameters, at least for experiments carried out in Florida during spring season. This standard cultivar should have a window for flowering between 23 to 28 days after transplanting

(depending on the age of the plant at transplanting) and it should reach physiological maturity between 85 to 95 days after transplanting. This is supported by our own observations during our 2006 and 2007 experiments and also by literature that reports a tomato cycle for fresh market cultivars growing in open field of 2 months from anthesis to maturation and three to four weeks from transplanting to anthesis (Jones, 1999; Mossler *et al*., 2005). If the crop is grown during fall, likely these times could be different and appropriate calibration may be necessary.

B) Parameters affecting leaf growth, dry matter (DM) production, and DM partitioning in the crop from the time transplanting to harvest were then calibrated against the observed data.

The model: The CROPGRO model used in this study is included in the DSSATV4.0 software. A complete description can be found in the software documentation, as well as in the paper published by Jones *et al*. (2003). The CROPGRO model simulates development based on seven phases, from emergence to harvest. Phenological development and some growth processes such as leaf expansion and fruit growth depend on the cardinal temperatures (Rinaldi *et al*., 2007). Moreover, leaf expansion depends on the new leaf mass produced and specific leaf area, which is determined by light, temperature, nitrogen, and water status. The carbon balance is mainly a function of intercepted light and leaf photosynthesis. The daily growth of tissues results from the gain of photoassimilates through photosynthesis minus respiration and growth maintenance losses. The allocation of assimilates among vegetative organs is driven by partitioning coefficients, but, once set, fruits have first priority sink strength. Although considered semi-determinate, the fresh market tomato cultivars grown under field conditions exhibit very low partitioning to vegetative sinks after the fruits begin their rapid growth phase. Thus, determinacy is simulated because the partitioning of assimilates to the reproductive sinks during the reproductive phase effectively causes leaf, stem, and root growth to terminate to the

limits of (1-XFRUIT), where XFRUIT is a parameter that determines how much of the available dry matter is allocated to the fruits (Boote and Scholberg, 2006). Sub models for nitrogen and water balance, as well as pest damage coupling simulations, are also available and can be switched on or off according to specific applications. The model requires three genetic files: species, ecotype, and cultivar files. The species file accounts for the sensitivity of crop processes to environmental factors such as temperature, solar radiation, CO_2, and photoperiod. The cultivar parameters define the life phase duration for each cultivar, and coefficients in the ecotype file represent traits that are common to groups of similar cultivars within species (Boote and Scholberg, 2006).

Literature search and file modifications: The default model (V4.0) uses the same cardinal temperature values for the three phenological phases (vegetative, early reproductive, and late reproductive phases), and those values are 10 ºC, 28 ºC, and 55 ºC for base, optimum (both $Topt_1$ and $Topt_2$), and Tmax, respectively. With the goal of improving temperature-dependent parameters in the CROPGRO-tomato model and after a literature search of cardinal temperatures for the species, the values published by Adams *et al*. (2001b) and reviewed in Chapter 2 are valuable because the study was carried out under environments in which the temperature was precisely controlled. Therefore, the adaptation of parameters for this work is based mainly on the data obtained by Adams *et al*., although the work of other authors is also considered. Table 3.1 summarizes the cardinal temperatures for both the default model and the modified values based on the literature for: phenological development, fruit addition and pollination, and shell and fruit growth of the tomato species.

Field data for calibration purposes: The growth data for calibration consisted of a series of eight experiments conducted between 1991 and 2007 at three locations in Florida: Bradenton,

Gainesville, and Quincy. Three experiments in Bradenton were conducted by McNeal *et al.* from 1991 to 1994. The treatments selected for calibration were well irrigated and well fertilized, and, therefore, no water or nitrogen stress was present. The soil utilized belongs to the Eaugallie fine sand family. The datasets for Bradenton 1995, Gainesville 1996, and Quincy 1995 were derived from field experiments conducted by Scholberg (1995, 1996) using irrigated tomatoes, and, excluding the Quincy studies, all experiments were carried out during the spring season. For Quincy, one dataset corresponded to the spring season and the other to the fall season. The Gainesville 2007 dataset was obtained from a field-grown plastic mulched fresh-market tomato experiment conducted in the spring of 2007, and the treatment selected for calibration was a well-fertilized and well-irrigated treatment. The soil consisted of fine sandy soil of the Millhopper series for Gainesville in 1996. For Gainesville in 2007, the soils were fine Candler sand and Tavares sand (Buster, 1979; Dukes *et al.* 2005). The Quincy soils belonged to the Orangeburg series. The treatment was drip irrigated, and the N application rate was 200 kg ha^{-1} at Gainesville, 180 kg ha^{-1} at Quincy (spring), and 200 kg ha^{-1} at Quincy (fall). For the simulations, the irrigation and N rates are not highly relevant because the N and water balance were turned off for all simulations.

The genotypes were *Sunny* for Bradenton, *Agriset* for Gainesville (1996), *Florida 47* for Gainesville (2007), and *Agriset* (spring) and *Solarset* (fall) for Quincy. However because similarities among cultivars, *Sunny*, which will be called standard hereafter, was calibrated for all the experiments except for Quincy during fall when the cultivar *Solarset* was grown and a different set of genetic parameters was calibrated for this cultivar.

Results and Discussion

Life phase duration: Decreasing the base temperature from 10ºC to 7ºC, as compared with the default values (Table 3-1), without changing the cultivar phase durations accelerated the

plant development rate and markedly shortened the life phase durations, as expected (data not shown). Tomato fruit growth, as supported by several authors, has a period of very slow growth which lasts about two weeks after anthesis (Mapelly *et al*., 1978; Varga and Bruisma, 1986; Boher and Banghert, 1988; Gillaspi *et al*., 1993; Heuvelink, 2005). This lag in fruit growth is not considered in the default version. In our calibration we account for this slow growth and modified one specie parameter called shell lag rate (SHLAG) changing its value from 0 to 0.1. The interpretation of this value is that during the days that immediately follow anthesis a single tomato fruit grows at a rate that is 10 % of the rapid growth phase (Dorais *et al*., 2001). This modification will be shown in the next chapters and was needed in order to appropriately model the growth of individual tomato fruits tagged at different dates.

Table 3-2 shows the results for the calibration of parameters in the ecotype file needed to readjust the life cycle (according our observations) and carbon balance after changing the cardinal temperatures in the specie file. The main changes in ecotype files are related to an increase in the required thermal time to complete vegetative phases. Furthermore, the rate of truss appearance was slightly reduced from 0.52 in the default version to 0.5 according to the De Koning (2000) data. The ecotype PM06 coefficient was also calibrated. In CROPGRO models, this parameter was developed for peanut. It represents a fraction of the time between first peg and first seed in the fruit during which the fruit grows slowly. If the PMO6 in the ecotype file is equal to 0.0, the first peg and the first fruit occur at the same time. If PMO6 is > 0.0, a slow growth phase occurs prior to the reported first fruit. In addition, the age of the plants at the time of transplanting was adjusted for each experiment (Table 3-3). For the simulation, plants were generally 1 to 3 days younger at the time of transplanting than used in the default version. The real age of plants for those experiments are not available and therefore the criteria for this

adjustment was a better phase duration adjustment when cardinal temperatures were updated considering that usually plant ages at transplanting range between three and four weeks in Florida production systems.

Tables 3-4 (standard cultivar) and 3-5 (*Solarset* cultivar), show the results of the parameter calibration performed to adjust the life cycle after entering the new cardinal temperatures in the specie file. The main changes in the cultivar file were the parameters that determine the phase durations. First, the timing of flower and fruit appearance was adjusted. The cultivar parameter EM-FL (days between plant emergence and flowering) was calibrated to a greater value, (it was increased by 11 %) in order to predict the anthesis date. Next to match the timing from flowering until the start of slow fruit growth, the cultivar coefficient FL-SH (thermal days between flowering and shell growth) was calibrated to a smaller value. The criteria for this calibration was that the model had to correctly predict the timing of flowering in order to simulate the development and growth over time of three cohorts whose development and growth began at different dates (separated by one week) based on the tagging dates. Our experiments during 2006 and 2007 indicated that first fruit were set 26 and 28 days after transplanting, respectively. As a consequence, our calibration process, in addition to the changes in cardinal temperatures, needed to calibrate to these observed fruit setting dates. Fruit set (small, but slow growing fruits) occurs within few days (FL-SH=3) after flowering. The ability of the model to correctly predict the time for first fruit is relevant for our purposes of improving the whole model and the fundamentals related to tagged individual fruit growth will be fully explained in Chapter 5. In addition, the cultivar coefficient FL-SD (time from flower to first seed) was increased by 18%. In order to improve the growth of fruits and seeds, the coefficients PODUR (duration of pod addition) and SFDUR (duration of seed filling) required calibration. These parameters were

increased by 18% and 4 %, respectively. In addition, in order to give more priority to shell growth over seed growth, the threshing percentage was slightly decreased. The coefficient SLAVAR (specific leaf area under standard growing conditions) was also slightly increased from 350 to 360.

After calibration, the model was able to reproduce the dates for anthesis, first fruits, and physiological maturity in our observations. This also agrees with literature showing that anthesis day occurs between 3 and 4 weeks after transplanting and that the whole life cycle from transplanting to harvest takes about 90 days. In addition the individual cohorts tagged at different dates during 2006 and 2007 seasons were adequately tracked by the model which was useful for later studies that we performed with the model (Chapter 5). The only exception was the 1995 Quincy experiment for the fall season in which the *Solarset* cultivar was grown. It was not possible to accurately calibrate this experiment because phenology data were not available. Therefore, for this cultivar a preliminary evaluation of the ability of the model to predict growth and yield data during fall season was done and the cultivar coefficients used are shown in Table 3-5. However, more plant phenology data will be necessary to adequately calibrate the *Solarset* cultivar to confirm our coefficient values.

Leaf area index: For most of the experiments, the progression of leaf growth was well simulated by the updated version (Figure 3-1 to 3-4). In general, the updated parameters demonstrated better performance for simulating LAI compared with the default version (Tables 3-6 and 3-7). Using the updated parameters the average error for all the experiments was 34% lower than using default values. The Willmott d index was higher using updated parameters than using the default ones (better correspondence between simulated and observed values). Nevertheless, the results still show two weaknesses in the model: 1) in both versions and for

several experiments, the maximum LAI was overestimated, and the only exceptions were Bradenton 1992 and 1994, for which LAI was underestimated. Because these differences, it is hard to obtain LAI simulations that satisfy the observations for all the experiments. In those years when LAI was overestimated, the model failed to reproduce the change in growth after the maximum LAI was attained. Therefore, the trend for early growth was relatively well simulated, although it displayed a small overestimation in the maximum LAI attained. Later in the season, the model, regardless of the version, was not able to efficiently reproduce the decay in leaf area associated with senescence and N remobilization. This may be fixed by adjusting the remobilization functions in the model, such as the maximum rate of remobilization of protein (NMOBMX) and carbohydrates (CMOBMX) from vegetative to reproductive tissues. These functions in CROPGRO determine how much N and C are remobilized according the age of the leaf, so if, for instance, the rates of remobilization are increased, leaf mass decline may occur naturally as a result of senescence. These changes were made (data not shown) but not used because while it improved LAI simulations for some experiments it made them worse in others. Overall the simulations were better leaving the remobilization functions unchanged.

Simulations of stem or leaf weight improved using the updated parameters (data not shown). The specific leaf area (SLA) was not very well simulated by the model, regardless of the version used. In addition, the Willmott d values for SLA were low, indicating that the variability in the mean SLA throughout the season was not well captured by the model. One possible explanation is that the model SLA depends basically on radiation and temperature. However, ontogenetic changes, nutrition, stresses are factors that may affect SLA a fact that is disregarded by the model.

Aboveground biomass and fruit yield: The total above biomass and fruit yield was well simulated using the updated parameters (Figures 3-5 to 3-12). On average, simulations using the updated parameters produced an RMSE that was 12 % lower for total biomass yield and for fruit yield as compared with the default version (Tables 3-6 and 3-7). Because the comparisons were made using time series data, the Willmott d index is a better indicator of model improvement. Overall, the d index was higher for total dry weight and fruit dry weight using updated parameters as compared with default parameters. On average, the d index for the updated version was 0.99 and 0.96 for total above biomass and fruit dry weight respectively, while the default version produced an average d value equal to 0.98 for total above biomass and 0.91 for total fruit weight.

Fruit number: The fruit number was well simulated by the model when updated parameters were used (Figures 3-13 to 3-15). The default version produced poor simulation of fruit number, always overestimating this variable with an average error equal to 33 fruits per square meter and a d value equal to 0.77 (Table 3-6). The error averaged over all experiments using the updated values was equal to 16 fruits per square meter and the average d value was 0.93 (Table 3-7). Averaged for all experiments the RMSE was 58% lower using the updated values comparing with the default version. The reason for the large PODUR (pod addition duration) value, is that the model computes this based on seed growth rate (demand) relative to assimilate supply. This feature is unrealistic for crops with low THRESH (ratio of seed to fruit plus seed).

Conclusions

After changing the cardinal temperatures for plant phenology using recently published data, it was necessary to increase the required thermal time for completing each phase in order to

predict the life cycle of the plant. The data obtained for transplant age are frequently absent or not recorded when field data are collected for calibration purposes. However, differences of two or three days for plant age at the time of transplanting are common in real practice and can significantly modify the phase duration in tomato, especially the thermal time accumulated from planting to anthesis, which, if calculated incorrectly, can propagate error to the other phases. Therefore, it is highly recommended that this information be documented when possible in order to obtain a correct calibration.

The results obtained for the LAI simulations suggested that the model still requires adjustments to correct the overestimation or underestimation of LAI depending on the experiment. In addition, in order to better adjust leaf growth, the model should be tested with cultivars that have both determinate and indeterminate growth. Until now, the model has only been calibrated with field data using near determinate cultivars growing in open field, and, therefore, assumptions regarding the behavior of the model in greenhouse conditions cannot be made until an appropriate evaluation is performed. It is anticipated that the way in which the model simulates the number and growth of stems should be studied and likely modified along with the growth of other sinks in the plant.

Overall, the ability of the CROPGRO-tomato model to simulate leaf growth, total biomass, and fruit dry weight yield based on the RMSE and Willmott d index values were improved using the updated version compared with the default version. Therefore, we recommend using the newly calibrated values of the genetic coefficients for the next release version of the CROPGRO-Tomato model. The proposed adaptation based on reliable values of cardinal temperatures should not only improve the accuracy of the tomato biomass and dry weight yield predictions but also reduce efforts in future model calibrations and evaluations.

Table 3-1. Parameters represent temperature dependence of tomato phenology, fruit and seed growth, default V4.0 values and updated values in specie file.

Parameter	Rate of leaf or truss appearance (vegetative development).	
	Default value (°C)	Updated value (°C)
T_b °C	10	7
T_{op1} °C	28	22
T_{op2} °C	28	28
T_{max} °C	55	48
	Rate of progress to anthesis /truss appearance (early reproductive growth)	
	Default	Updated
T_b °C	10	7.2
T_{op1} °C	28	22
T_{op2} °C	28	28
T_{max} °C	55	48
	Rate of fruit development and maturation (late reproductive growth)	
	Default	Updated
T_b °C	10	5.7
T_{op1} °C	28	26
T_{op2} °C	28	28
T_{max} °C	55	48
	Relative effect of temperature on rate of fruit addition and pollination.	
	Default	Updated
T_b °C	6	7.2
T_{op1} °C	8	22
T_{op2} °C	28	25.5
T_{max} °C	30	32
	Relative effect of temperature on rate of individual seed/fruit growth.	
	Default	Updated
T_b °C	6	6
T_{op1} °C	8	22
T_{op2} °C	25.5	25
T_{max} °C	32	32

Table 3-2. Additional modified parameters in ecotype file, default V4.0 values and calibrated values.

Parameter	Default value	Calibrated value
Time between planting and emergence PL-EM (Td)**	5	6
Time between emergence and first true leaf EM-V1 (Td)	20	22
Time required for growth of individual fruit LNGSH (Td)	35	39
Time between first flower and last leaf in main stem FL-VS (Td)	18	23
PMO6, if PM06 is 0.0, first peg and first pod occur at the same time. If PMO6 > 0.0 there is a slow growth phase	0.0	0.6
Rate of leaf appearance on main stem, TRIFL	0.52	0.5
Maximum ratio of (seed/(seed+shell)) at maturity THRSH (%)	9.2	8.5

**Td=thermal days

Table 3-3. Tomato plant age at transplanting in CROPGRO default V4.0 values and calibrated values in experimental file (X).

Experiment	Default	Calibrated
Bradenton 1991	28	25
Bradenton 1992	28	25
Bradenton 1994	28	26
Bradenton 1995	28	25
Quincy 1995 (spring)	28	26
Quincy 1995 (fall)	28	25
Gainesville (1996)	28	26
Gainesville (2007)	28	28

Table 3-4. Cultivar coefficients in CROPGRO-Tomato model, default and calibrated values after updating the cardinal temperatures in SPE file. Standard cultivar.

Parameter	Definition	Default	Calibrated
EM-FL	Time between plant emergence and flower appearance (R1) (thermal days)	23	25
FL-SH	Time between first flower and first pod (R3) (thermal days)	8	3.0
FL-SD	Time between first flower and first seed (R5) (thermal days)	17	20
SD-PM	Time between first seed (R5) and physiological maturity (R7)	50	50
FL-LF	Time between first flower (R1) and end of leaf expansion (thermal days)	50	50
LFMAX	Maximum leaf photosynthesis rate at 30 C, 350 vpm CO2, and high light (mg CO2/m2-s)	1.36	1.36
SLAVR	Specific leaf area of cultivar under standard growth conditions (cm2/g)	350	360
SIZLF	Maximum size of full leaf (three leaflets) (cm2)	300	300
XFRUT	Maximum fraction of daily growth that is partitioned to seed + shell	0.75	0.75
WTPSD	Maximum weight per seed (g)	0.0040	0.0040
SFDUR	Seed filling duration for pod cohort at standard growth conditions (thermal days)	25	26
SDPDV	Average seed per pod under standard growing conditions (#/pod)	300	300
PODUR	Time required for cultivar to reach final pod load under optimal conditions (thermal days)	42	55

Table 3-5. Cultivar coefficients in CROPGRO-Tomato model, default and calibrated values after updating the cardinal temperatures in SPE file. Cultivar: *Solarset.*

Parameter	Definition	Default	Calibrated
EM-FL	Time between plant emergence and flower appearance (R1) (thermal days)	23	32
FL-SH	Time between first flower and first pod (R3) (thermal days)	8	5.0
FL-SD	Time between first flower and first seed (R5) (thermal days)	17	22
SD-PM	Time between first seed (R5) and physiological maturity (R7)	50	52
FL-LF	Time between first flower (R1) and end of leaf expansion (thermal days)	50	52
LFMAX	Maximum leaf photosynthesis rate at 30 C, 350 vpm CO2, and high light (mg CO2/m2-s)	1.36	1.36
SLAVR	Specific leaf area of cultivar under standard growth conditions (cm2/g)	350	360
SIZLF	Maximum size of full leaf (three leaflets) (cm2)	300	300
XFRUT	Maximum fraction of daily growth that is partitioned to seed + shell	0.75	0.75
WTPSD	Maximum weight per seed (g)	0.004	0.004
SFDUR	Seed filling duration for pod cohort at standard growth conditions (thermal days)	25	26
SDPDV	Average seed per pod under standard growing conditions (#/pod)	300	300
PODUR	Time required for cultivar to reach final pod load under optimal conditions (thermal days)	42	60

Table 3-6. Root mean square error and Willmott d index for simulations using default genetic parameter values.

Experiment	Leaf Area Index		Total Above Biomass		Total Fruit Weight		Fruit Number	
	RMSE	d	RMSE	d	RMSE	d	RMSE	d
BR1991	0.91	0.9	447	0.99	678	0.95	42	0.70
BR1992	0.81	0.93	449	0.99	282	0.99	34	0.88
BR1994	1.10	0.92	1040	0.98	874	0.97	51	0.75
BR1995	0.88	0.89	658	0.99	772	0.87	nd	
QU1995 (S)	0.97	0.95	886	0.97	629	0.97	nd	
QU1995 (F)	0.36	0.96	485	0.98	697	0.93	nd	
GA1996	1.14	0.87	445	0.99	519	0.86	31	0.76
GA2007	1.66	0.79	656	0.99	667	0.79	37	0.78
Average	**0.98**	**0.90**	**633**	**0.98**	**639**	**0.91**	**39**	**0.77**

Table 3-7. Root mean square error and Willmott d index for simulations using updated genetic parameter values.

Experiment	Leaf Area Index		Total Above Biomass		Total Fruit Weight		Fruit Number	
	RMSE	d	RMSE	d	RMSE	d	RMSE	d
BR1991	0.45	0.98	645	0.99	856	0.94	12	0.85
BR1992	1.0	0.85	686	0.99	576	0.99	12.6	0.97
BR1994	1	0.88	720	0.99	712	0.985	23	0.93
BR1995	0.76	0.91	440	0.99	516	0.92	nd	
QU1995 (S)	0.32	0.99	391	0.99	572	0.97	nd	
QU1995 (F)	0.69	0.93	633	0.99	583	0.95	nd	
GA1996	0.5	0.96	604	0.99	510	0.96	9	0.96
GA2007	0.43	0.97	330	0.99	178	0.99	23	0.91
Average	**0.65**	**0.93**	**556**	**0.99**	**562**	**0.96**	**16**	**0.92**

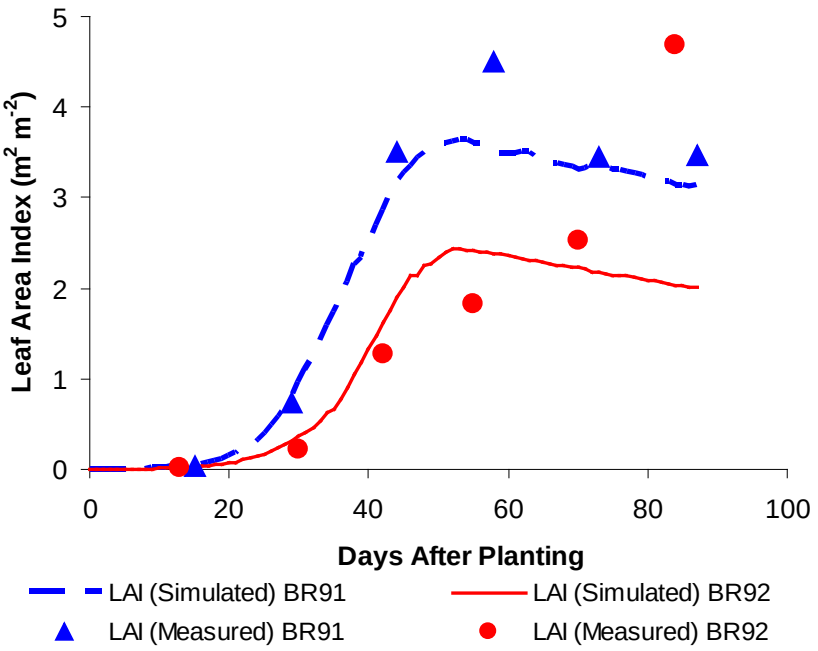

Figure 3-1. Simulated and observed Leaf Area Index for tomato standard cultivar in Bradenton, Fl during spring of 1991 and 1992 using updated parameters (Table 3-4).

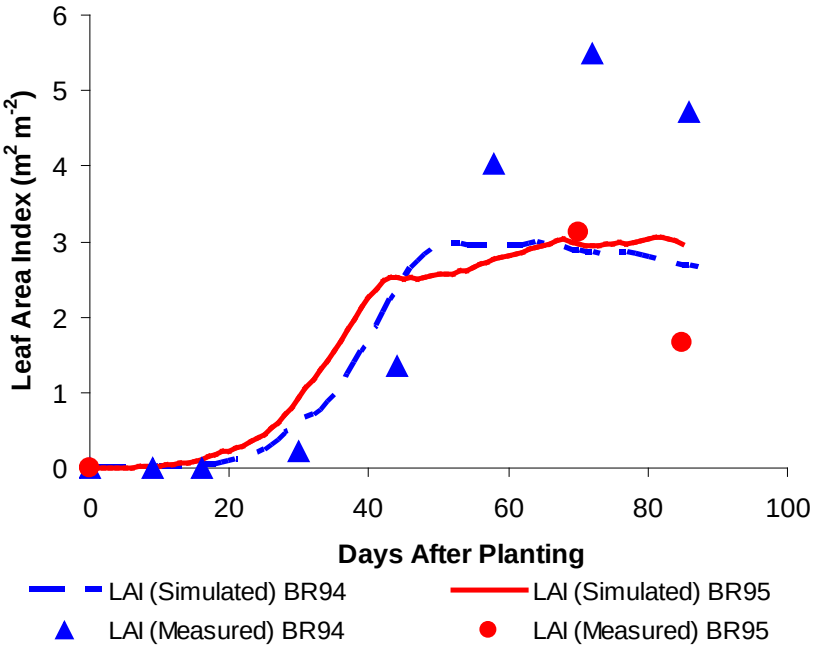

Figure 3-2. Simulated and observed Leaf Area Index for tomato standard cultivar in Bradenton, Fl during spring of 1994 and 1995 using updated parameters (Table 3-4).

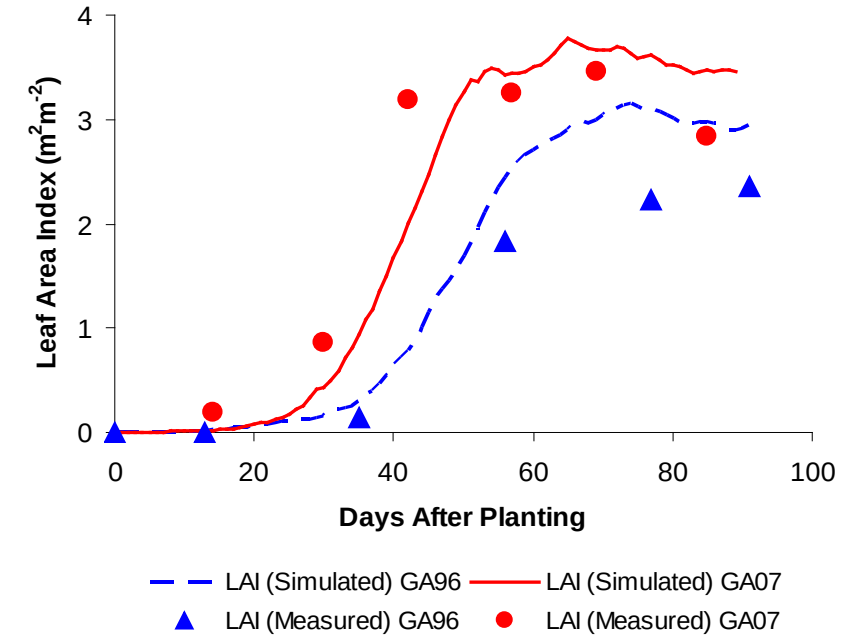

Figure 3-3. Simulated and observed Leaf Area Index for tomato standard cultivar in Gainesville, Fl during spring of 1996 and 2007 using updated parameters (Table 3-4).

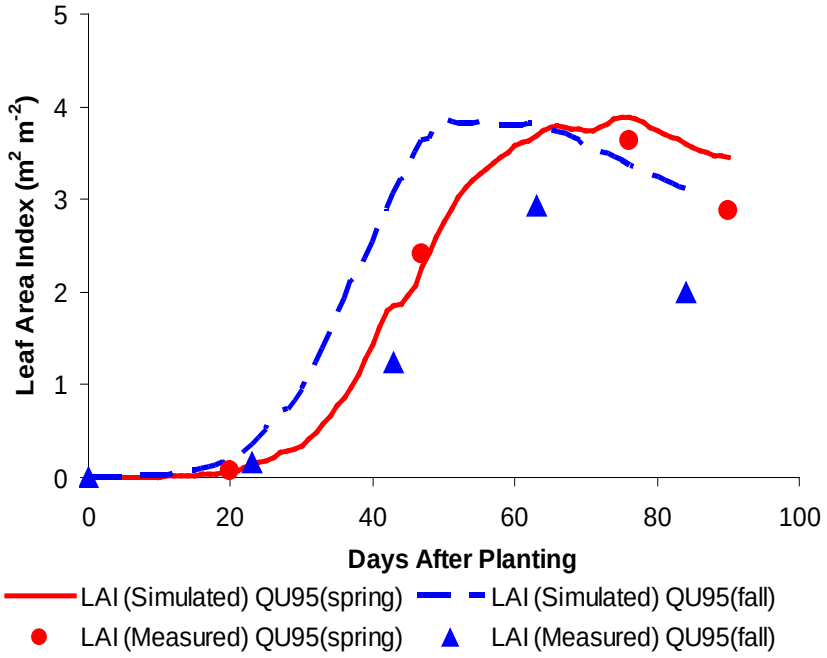

Figure 3-4. Simulated and observed Leaf Area Index for tomato in Quincy, Fl during 1995 standard cultivar (spring) and S*olarset* cultivar (fall) using updated parameters (Table 3-4).

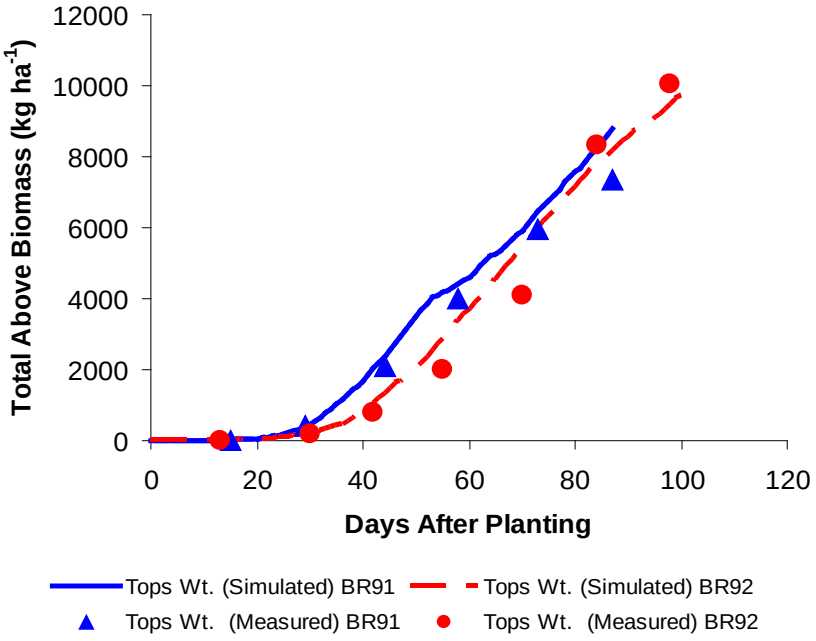

Figure 3-5. Simulated and observed total above biomass for tomato standard cultivar in Bradenton Fl, during spring of 1991 and 1992 using updated parameters (Table 3-4).

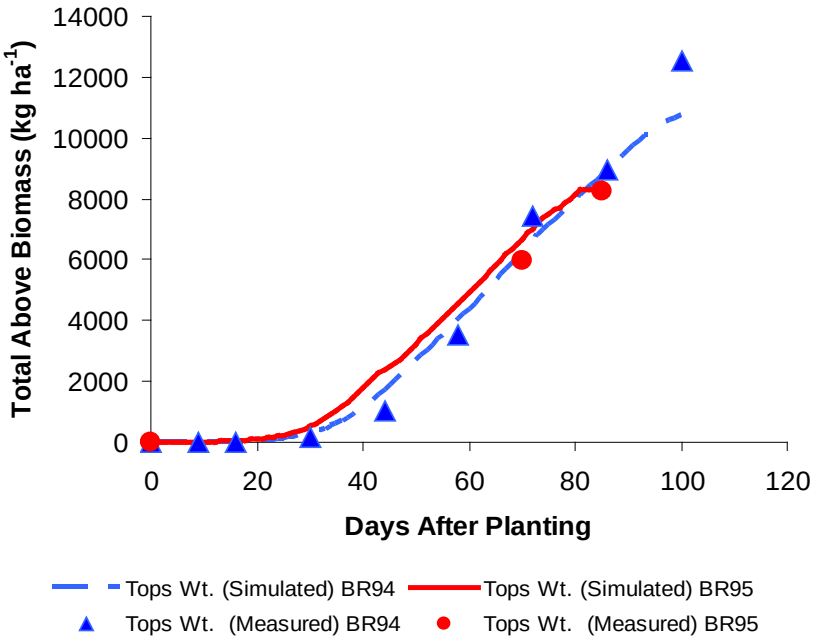

Figure 3-6. Simulated and observed total above biomass for tomato standard cultivar in Bradenton, Fl during spring of 1994 and 1995 using updated parameters (Table 3-4).

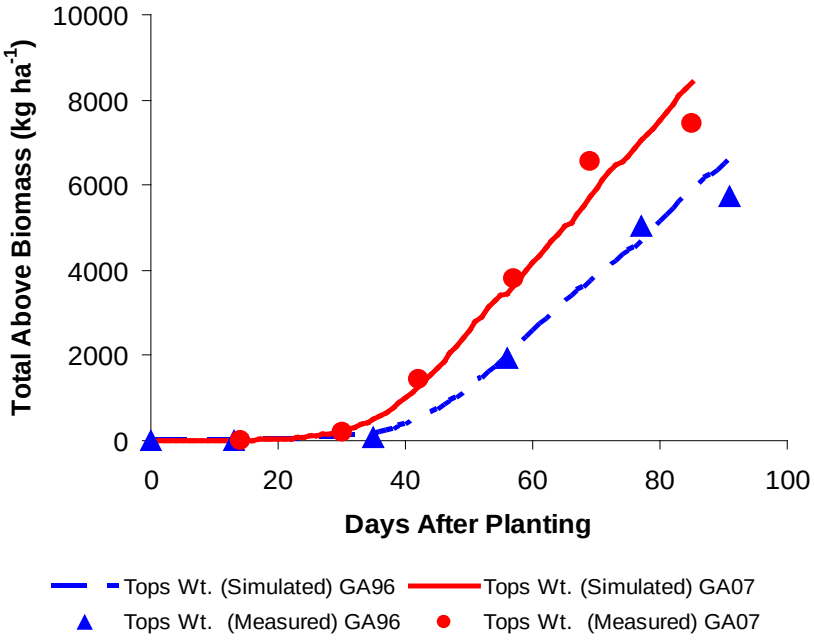

Figure 3-7. Simulated and observed total above biomass for tomato standard cultivar in Gainesville, Fl during spring of 1996 and 2007 using updated parameters (Table 3-4).

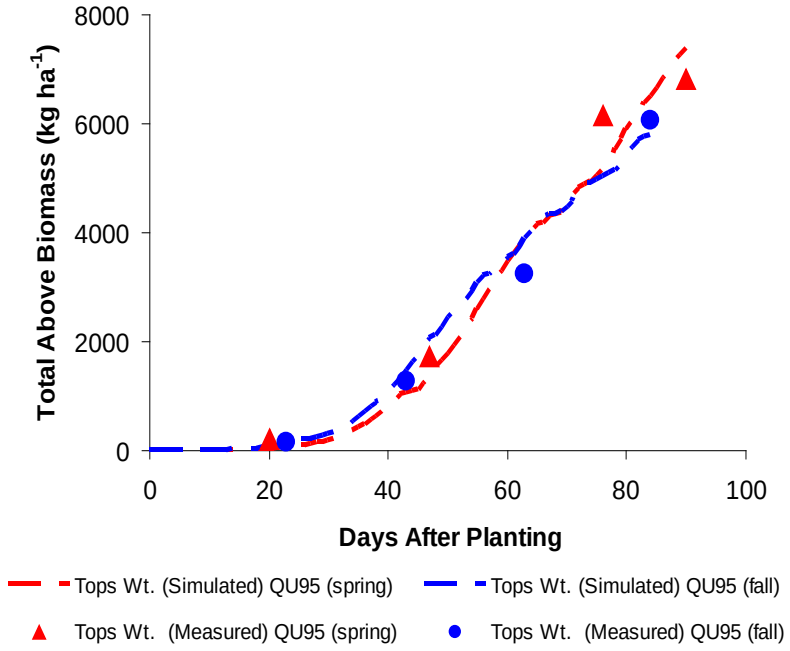

Figure 3-8. Simulated and observed total above biomass for tomato in Quincy, Fl during 1995 standard cultivar (spring) and S*olarset* cultivar (fall) using updated parameters (Table 3-4 and 3-5).

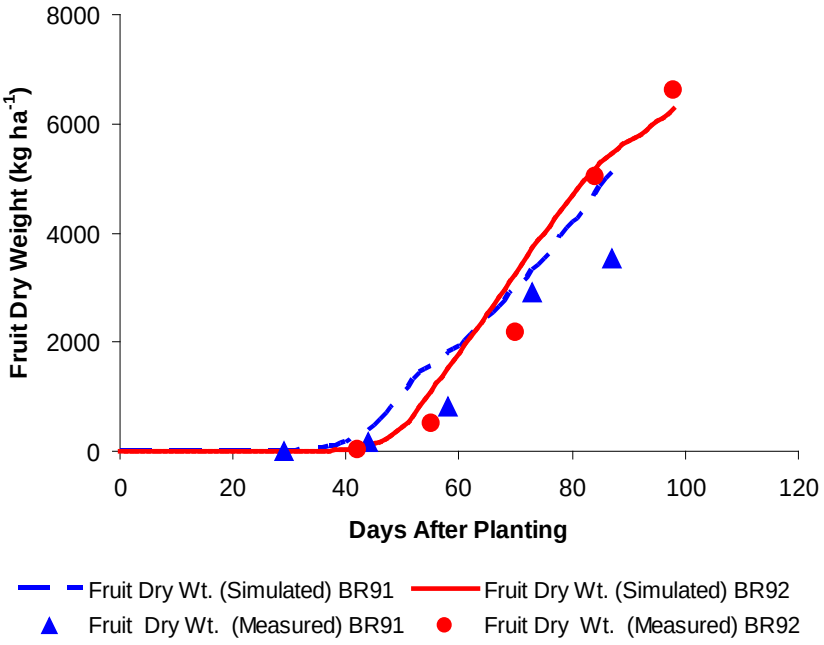

Figure 3-9. Simulated and observed total fruit dry weight for tomato standard cultivar in Bradenton, Fl during spring of 1991 and 1992 using updated parameters (Table 3-4).

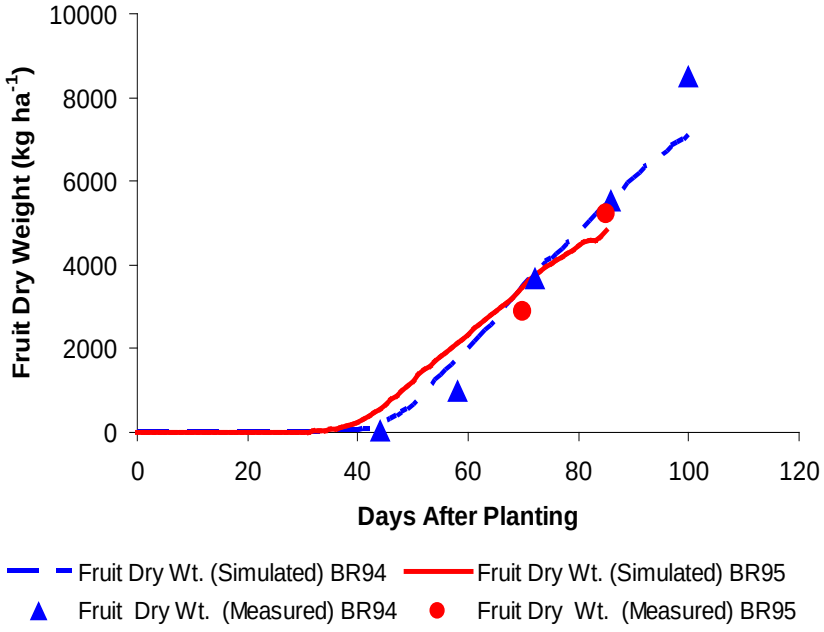

Figure 3-10. Simulated and observed total fruit dry weight for tomato standard cultivar in Bradenton, Fl during spring of 1994 and 1995 using updated parameters (Table 3-4).

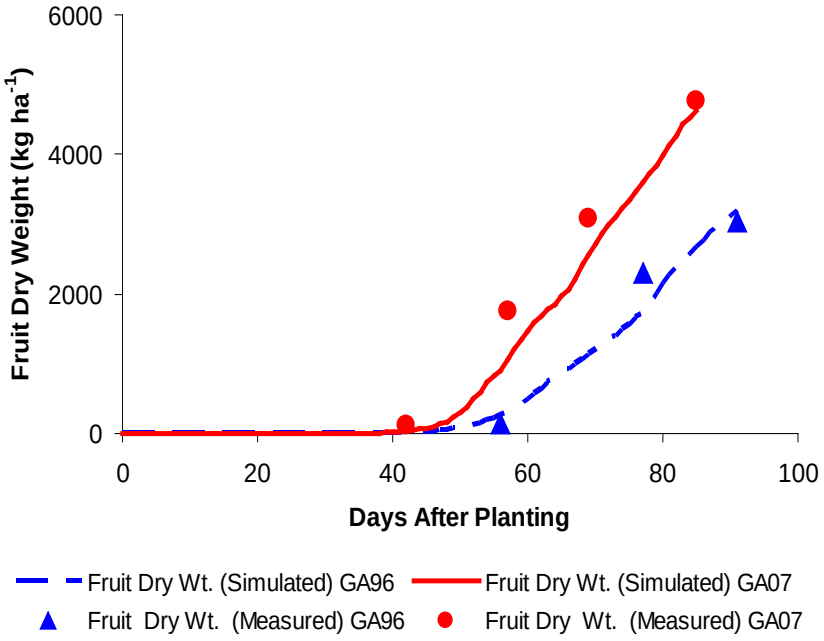

Figure 3-11. Simulated and observed total fruit dry weight for tomato standard cultivar in Gainesville, Fl during spring of 1996 and 2007 using updated parameters (Table 3-4).

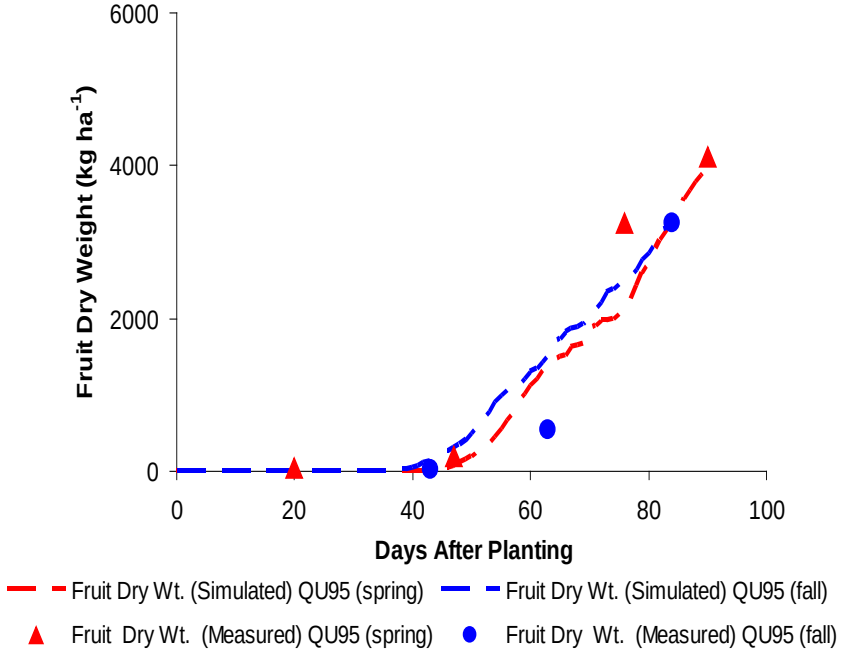

Figure 3-12. Simulated and observed total fruit weight for tomato in Quincy, Fl during 1995 standard cultivar (spring) and S*olarset* cultivar (fall) using updated parameters (Table 3-4 and 3-5).

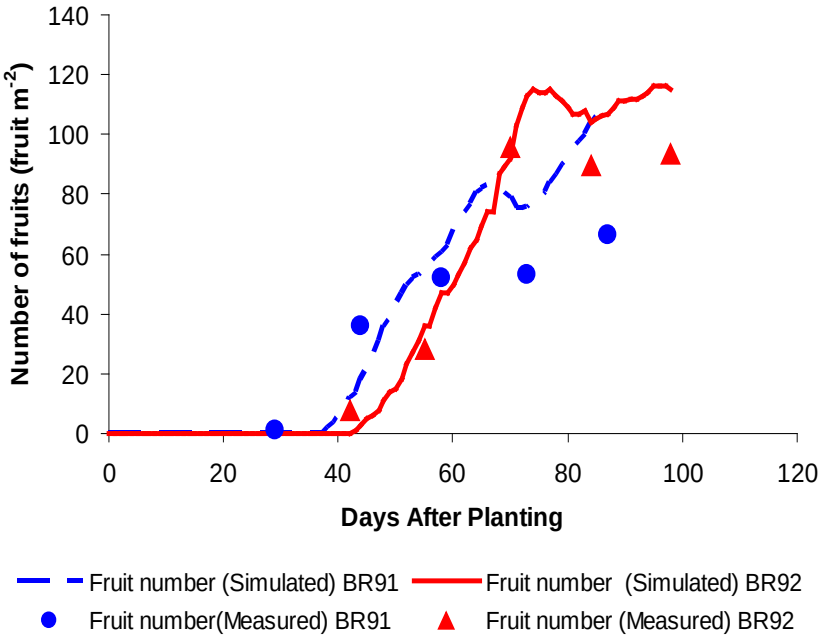

Figure 3-13. Simulated and observed fruit number for tomato standard cultivar in Bradenton, Fl during spring of 1991 and 1992 using updated parameters (Table 3-4).

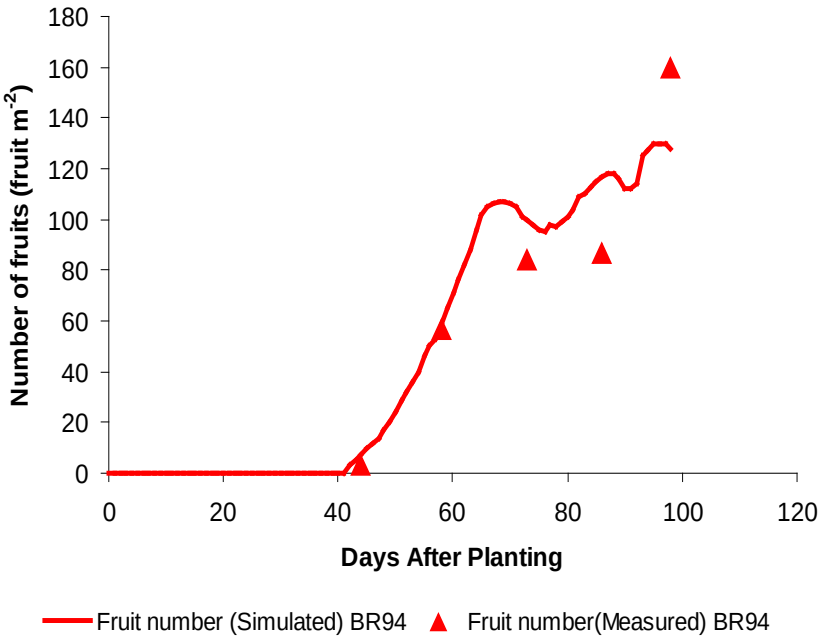

Figure 3-14. Simulated and observed fruit number for tomato standard cultivar in Bradenton, Fl during spring of 1994 using updated parameters (Table 3-4).

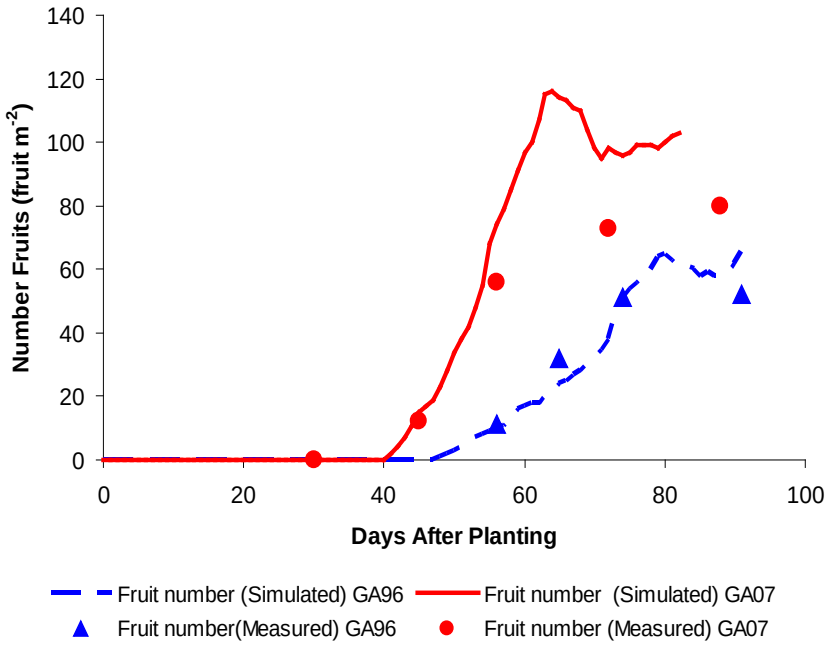

Figure 3-15. Simulated and observed fruit number for tomato standard cultivar in Gainesville, Fl during spring of 1996 and 2007 using updated parameters (Table 3-4).

CHAPTER 4
EQUATIONS FOR GROWTH OF TOMATO FRUITS UNDER NON-LIMITING CONDITIONS

Introduction

Several authors have reported that the potential growth of individual tomato fruit exhibits a simple sigmoid or S shaped curve (Gustafson, 1926; Nitsh 1953; Coombe, 1976; Monselise *et al*. 1978; Wolf and Rudich, 1988; Gillaspi *et al*., 1993; Chamarro, 1995, Ho and Hewitt, 1986; Heuvelink, 2005). This curve is characterized by three phases. The growth is slow immediately after fertilization, increases gradually to a maximum rate, and finally decreases as the fruit approaches maturation. During the first stage of fruit development, cell division and enlargement result in slow growth. Following fertilization in the tomato, cell division is activated in the ovary and continues for about 2 weeks (Mapelly *et al*., 1978; Varga and Bruisma, 1986; Boher and Banghert, 1988; Gillaspi *et al*., 1993; Heuvelink, 2005). After ~2-3 weeks of slow growth, rapid growth begins. During this time, the cells continue to enlarge by cell expansion. Rapid growth continues for ~3-5 weeks, culminating in the mature green stage. At this point, the tomato has accumulated the majority of its final weight (Ho and Hewitt, 1986). Finally, when the biochemical changes related to ripening begin, growth becomes slow again. Approximately ten days before the first break of color, growth ceases completely. This occurs because an abscission layer is formed between the calyx and the fruit, which becomes a barrier to the transport of water and assimilates to the fruit (Heuvelink, 2005).

Theoretical growth functions have been widely used to study plant growth. The construction of growth curves is a valuable tool for dynamic analysis of fruit growth behavior, and growth curves may provide a knowledge base for modeling purposes. Any growth variable, e.g. dry weight, fresh weight or fruit diameter, can be plotted as a function of time. Additionally, if growth is analyzed as a function of the physiological age of the fruit rather than of the calendar

time, then temperature is incorporated into the analysis, enhancing the predictive value of the growth curves.

Regression analysis is a mathematical tool to establish the relationship between two variables (Steel and Torrie, 1992). For the tomato, nonlinear regression has been used to develop models of fruit growth. The two adjusted models that are often reported to successfully fit the sigmoid-shaped growth of tomato fruit are the logistic model (Gustafson, 1927; Calado *et al.*, 1980; Monteiro, 1983; He and Zhang, 2006) and the Gompertz function (De Koning, 1994; Bertin, 1995; Adams *et al*., 2001; Enriquez *et al*., 2005; Bertin *et al*., 2008). According to Bertin *et al.* (2008), the Gompertz function is more appropriate than the logistic model to describe the growth of tomato fruit, because the Gompertz function better accounts for the slow increase in size at the start of the growth period. The Gompertz function is suitable for a sigmoid growth curve in which growth is frequently not symmetrical about an inflection point, i.e., when the relative growth rate (RGR) decreases with time (Erickson, 1976), as has been shown for tomato by Monselise *et al*. (1978).

A sigmoid growth function ideally originates at (0,0), with a point of inflection occurring early in the growth period, and either asymptotically approaches a maximum value or peaks and falls in the senescent phase (Khamis *et al*., 2005). Several criteria are used to compare alternative models of nonlinear regression. In general, the preferred model is the one that has a lower mean square error (MAE), a smaller number of parameters (simplicity principle), and a lower standard error (SE) of the estimates (Infostat, 2002). Examples of mathematical functions used to analyze fruit growth of horticultural crops can be found in Marcelis *et al.* (1998). In addition to time, environmental factors that have a strong influence on growth may be used to model growth curves. Lakso *et al.* (1995) have tested the use of the expolinear model of Goudriaan and

Monteith (1990), to simulate the growth of apple fruits (Opara, 1999). This model has three parameters: the maximum absolute growth rate (weight gain per day reached in the linear phase), the relative growth rate (weight gain per unit weight per day), and the x-axis intercept of the linear growth phase, called the "lost time". The expolinear model provides a good fit to the growth patterns of two apple cultivars that differ in their rates of growth during the exponential phase due to differences in crop load (Lasko *et al.*, 1995). This fact could be very useful in tomato, because tomato growth is characterized by considerable variation in sink strength among fruits (De Koning, 1989; Bertin, 1995; Bruchon and Genard, (1999). Ho (1992) found that the dry matter distribution in tomato fruits is strongly linked to the date of fruit initiation. De Koning (1989) has observed that individual tomato fruit growth is delayed when the competition for assimilates is high, and that delayed fruits started to grow again when the first trusses reached maturity. To explain this phenomenon, Bertin (1995) used the term “fruit delay” or “fruit latency” to describe fruits that have been set but whose growth and development are delayed during their early stage. These fruits reassume their growth after a delay of 10 to 50 days, when the first fruits of the earlier inflorescences have ripened. Moreover, although these delayed fruits come to maturity, their final size is smaller than that of the earlier fruits. The results of Bertin (1995) agree with those of other authors who have also observed this fruit growth latency caused by competition for assimilates (Ho, 1984; Picken, 1984; Wolf and Rudich 1988; De Koning, 1989). In addition, Bertin (1995) has experimentally verified that the delay is not produced by parthenocarpy, but is due to competition for assimilates among fruits in a truss and especially among trusses, with earlier fruits having higher sink strength than later fruits. In addition, Monteiro (1983) has reported that the growth rates of tomato fruits of different ages are significantly different.

The objective of this chapter is to examine the growth of individual tomato fruits whose development began on different dates.

Materials and Methods

Field data: The growth data for evaluation were obtained from experiments conducted in field-grown, plastic-mulched fresh-market tomato plots between April and July of 2006 and repeated in 2007. The experimental area was located at the University of Florida Plant Science Research and Education Unit at Citra, Florida (29º 25' N, 82º 10' W). The treatment selected for evaluation of fruit growth was well irrigated and fertilized; therefore, no water or nitrogen stress was present at any time during the growing season. The soil at this site is classified as Candler fine sand and as Tavares sand (Buster, 1979; Dukes et al. 2005). These soils contain 97% sand-sized particles and have a field water holding capacity of 5.0% to 7.5% by volume in the upper 100 cm of the profile (Carlisle et al., 1988; Dukes et al., 2005). The cultivar evaluated was Florida 47, a mid- to late-season hybrid whose fruits are deep globe shaped.

Each replicate plot consisted of four 15.2 m-long rows in completely mulched, fumigated beds, into which 4-wk old plants were transplanted on April 04 in 2006 and April 07 in 2007. Row spacing was 1.83 m and plant spacing was 0.45 m, making a total of 11,960 plants ha^{-1}.

Pre-planting fertilizer applications were 112 kg P2O5 ha^{-1} and 45 kg K2O ha^{-1}. Treatments were replicated four times using a randomized complete block design. Water application was based on calculated crop evapotranspiration (ET). Nitrogen application rates were based on IFAS recommendations, consisting of 224 kg N ha^{-1}, which was applied with the irrigation water. Irrigation was applied with a drip tape system; emitters were spaced 20 cm apart. Climatic data, including temperature, solar radiation, rainfall, wind and humidity, were collected by an automatic weather station located within 1 km of the experimental area.

Growth analysis of individual fruits: Three sets of flowers separated by one week in age were tagged at anthesis. For each cohort date, at least 60 flowers were tagged in each replicate (modified from Heuvelink, 1995). Starting 3 days after anthesis, and two times per week, two tagged fruits in each plot were randomly sampled at 08.00 h in the morning. Therefore, samples were collected at 3, 7, 11, 14, 18, 22, 26, 30, 33, 37, 41, 45, 49 and 53 days after tagging. For each sampled fruit, the fruit diameter was measured, the fresh weight (FW) was recorded, and the dry weight (DW) was determined. The experimental data on fruit growth (DW, FW, and fruit diameter) were fitted to three parameters of the Gompertz function in order to analyze the fruit growth as a function of time (Bertin, 1995). The data on fruit dry matter concentration (DMC) were fitted to a four parameter Gompertz function with displacement for analysis of DMC variation over time.

Results and Discussion

Fruit dry weight and fresh weight growth: Figures 4-1, 4-2, 4-3 and 4-4 present the experimental data for individual tomato fruits (DW, FW, dry matter concentration (DMC) and fruit diameter) measured during the year 2007 and show their fit to parameters of the Gompertz functions given in Table 4-1. The growth of tomato fruits in DW, FW and diameter was well described by the Gompertz function. The best relationship was for cohort 1. Cohorts 2 and 3 have a similar mean square error (MAE) and standard error (SE) to those of cohort 1 for the coefficients α and γ; however, the SE of the parameter β was higher in the adjustment of cohorts 2 and 3 (Table 4-1), showing that β is the parameter with the greatest uncertainty. The parameter α closely followed the final fruit dry weight, fresh weight or diameter. Tomato fruits showed the classical sigmoid growth curve, albeit with a nearly linear middle phase (Figures 4-1, 4-2 and 4-3). Growth began with a phase of slow growth for a few days after anthesis, then increased to an almost linear slope for about 4 to 5 weeks, and then slowed again close to maturation. As shown,

the curves are largely convex but have a lag period lasting between 9 and 14 days, depending on the cohort. The lag periods were shorter for earlier than for later cohorts. Similar results were obtained when the 2006 data was fitted to a Gompertz function (data not shown). The DMC data of 2007 were fit better by a four-parameter Gompertz function with displacement than by a simple Gompertz function. These results are shown in Table 4-1 and Figure 4-4.

Measured fruit growth: The observed differences in the final fresh weights, dry weights and fruit diameters of fruits whose development began on different dates are presented in Table 4-2. The total dry and fresh weight differed significantly among cohorts. Fruits that developed from flowers tagged earlier (first cohort) achieved the highest mass (both dry and fresh). Fruits from the second cohort achieved lower final mass than those of the first cohort, but higher final mass than those of the third cohort. In addition, the difference between cohorts 1 and 2 was much smaller than the difference between cohorts 1 and 3, indicating very slow growth of the latest setting fruits. These differences among cohorts in the final fresh and dry weights are partly attributable to differences in the length of the fruit growth period, which was 53 days for cohort 1, 46 days for cohort 2 and 37 days for cohort 3.

In addition, there were differences among cohorts in the rate of growth. The rate of dry mass accumulation estimated from the first derivative of the Gompertz function shows that the three cohorts did not have the same growth rate (Figure 4-5). The maximum growth rate was reached relatively earlier in cohort 1, occurring on day 22, which represents about 40% of the total growth period. Cohort 2 also reached the maximum growth rate on day 22, representing about 45% of the total fruit growth period. Similarly, Bertin (1995) and Dorais *et al*. (2001) have reported that the maximum growth rate in tomato fruits is reached by day 21 to 25 after anthesis. A larger lag was seen in cohort 3. For this cohort, the maximum growth rate occurred on day 26,

after almost 63% of the total fruit growth period. Figure 4-5 shows how the latest set fruits, after overcoming their long initial lag phase, reached a relatively high maximum growth rate. This indicates that growth accelerated during the phase of rapid growth in this cohort. Values of tomato fruit maximum growth rate reported in the literature range from 0.2 g dry matter d^{-1} (Jones *et al*. 1991) to 0.37 g dry matter d^{-1} (Dorais *et al*, 2001). However, Bertin (1993) has reported a value as high as 1.04 g dry matter d^{-1}. Variation in growth rate among cohorts has also been reported by Monteiro (1983), Ruddich and Wolf (1988) and Bertin (1995), who found that the rate of dry matter accumulation was significantly different among fruits initiated on different dates.

Fruit dry matter concentration: The final fruit dry matter concentration was similar for the three cohorts, and no significant differences were found among them (Table 4-2). However, the fact that a modified Gompertz function (with displacement) was needed for a better fit indicates that the pattern of dry matter concentration varied among cohorts, and that this variation was related to the timing of fruit initiation.

Fruit size: The mean final fruit size differed significantly among cohorts, as shown in Table 4-2. Fruits that developed from flowers tagged earlier achieved the greatest diameter. The fruits that developed from the second cohort achieved smaller diameters than those of the first cohort, but were much larger than fruits from the third cohort. These differences might be attributable to the same factors proposed to explain the differences among cohorts in final fresh and dry weights. In addition, during the 2007 growing season, fruits from cohort 3 did not reach commercial size.

Conclusion

The growth of individual tomato fruits expressed in terms of dry weight, fresh mass or fruit size follows a sigmoid curve, and is well represented by a three-parameter Gompertz function.

This function is adequate to reproduce the lag in the growth of tomato fruits early in the cycle (between one and two weeks after anthesis, depending on the cohort). Differences in growth are mainly related to the timing of initiation of the fruits, which determines the duration of the growth period. The sink strength of earlier-set fruits appears to be stronger than that of later-set fruits.

The dry matter concentration is better represented by a four-parameter Gompertz function than by the classical three-parameter function. However, the four-parameter in the function shows greater uncertainty, as evidenced by the higher S.E. of the estimates for the second and third cohorts.

Table 4-1. Estimated coefficients solved by fitting the 2007 data to a Gompertz function to predict DW, FW and fruit diameter.

Parameter	Fruit Dry Weight (g) = alpha*exp(-beta*exp(-gamma*DAT))					
	Cohort 1	S.E	Cohort 2	S.E	Cohort 3	S.E
α	15.31	0.69	9.22	0.42	6.2	0.39
β	5.98	1.00	124	13.7	99	75
γ	0.08	0.01	0.23	0.07	0.17	5.43
Parameter	Fruit Fresh Weight (g) = alpha*exp(-beta*exp(-gamma*DAT))					
	Cohort 1	S.E	Cohort 2	S.E	Cohort 3	S.E
α	313	11.13	183	6.13	87.0	5.39
β	8.13	1.48	289	290	257	200
γ	0.09	0.01	0.25	0.04	0.20	0.03
Parameter	Fruit Diameter (cm) = alpha*exp(-beta*exp(-gamma*DAT))					
	Cohort 1	S.E	Cohort 2	S.E	Cohort 3	S.E
α	11.47	0.41	7.65	0.19	4.39	0.61
β	8.54	1.46	68.5	33.0	39.94	27.5
γ	0.09	0.01	0.20	0.02	0.09	0.01
Parameter	Fruit DMC (%) = alpha*exp(-beta*exp(-gamma*DAT))+delta					
	Cohort 1	S.E	Cohort 2	S.E	Cohort 3	S.E
α	108	0.84	121	0.71	47	14.7
β	1.15	1.97	1.36	1.36	0.03	2.16
γ	0.01	0.01	0.02	0.02	0.02	6.8
δ	0.09	0.09	0.14	35.4	0.19	33

Table 4-2. Means comparisons among cohorts for dry weight, fresh weight, dry matter concentration and fruit diameter of individual tomato fruits, measured during the spring of 2006 and 2007 at Gainesville, FL.

Cohort	Measured data, 2006	Measured data, 2007
	DW g fruit $^{-1}$	DW g fruit $^{-1}$
1	10.8 a	13.6 a
2	7.9 b	9.1 b
3	6.3 c	3.6 c
	FW g fruit $^{-1}$	FW g fruit $^{-1}$
1	224 a	279 a
2	173 b	172 b
3	154 c	72 c
	DMC (%)	DMC (%)
1	4.8 a	5.0 a
2	4.7 a	4.9 a
3	4.9 a	4.8 a
	Fruit Diameter (cm)	Fruit Diameter (cm)
1	9.0 a	10.4 a
2	7.2 b	7.5 b
3	3.9 c	3.3 c

Test: $\alpha = 0.05$. Different letters indicate significant differences among cohorts ($p <= 0.05$). Each value is a mean of four fruits.

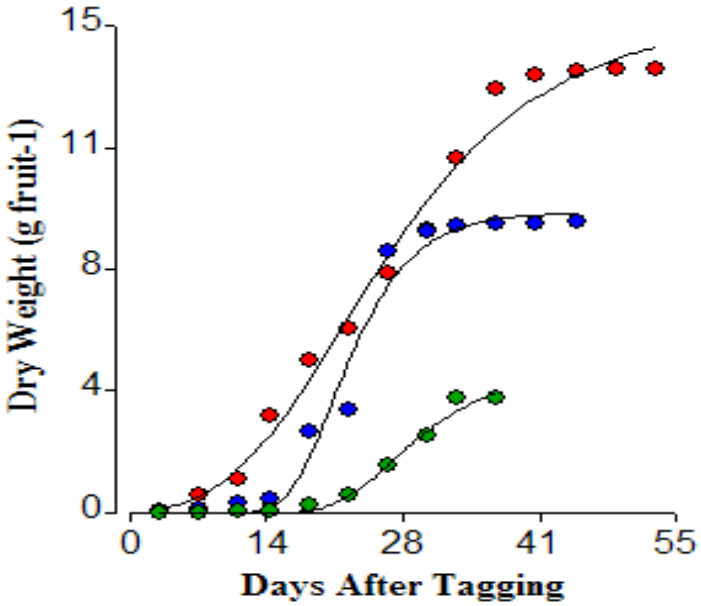

Figure 4-1. Individual fruit growth curves (g dry matter per fruit) over time in 2007, fitted to a three-parameter Gompertz function (●Cohort 1, ●Cohort 2, ●Cohort 3). Each point is a mean of four fruits.

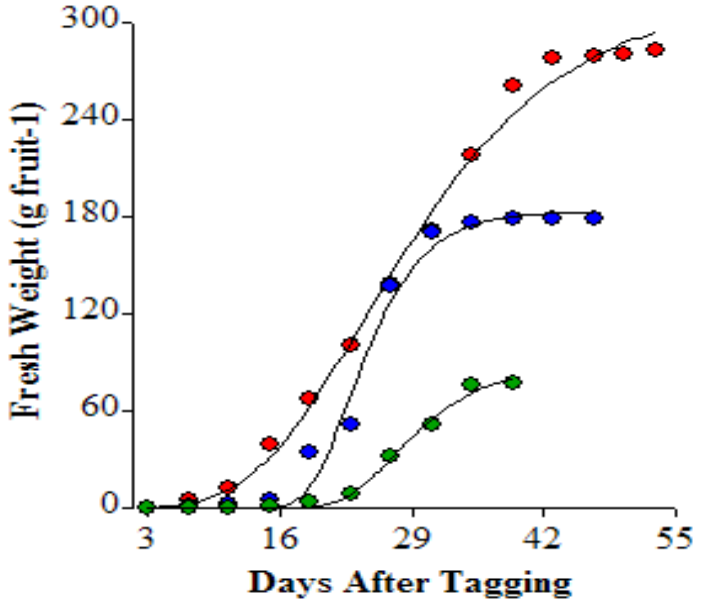

Figure 4-2. Individual fruit growth curves (g fresh mass per fruit) over time in 2007, fitted to a three-parameter Gompertz function (●Cohort 1, ●Cohort 2, ●Cohort 3). Each point is a mean of four fruits.

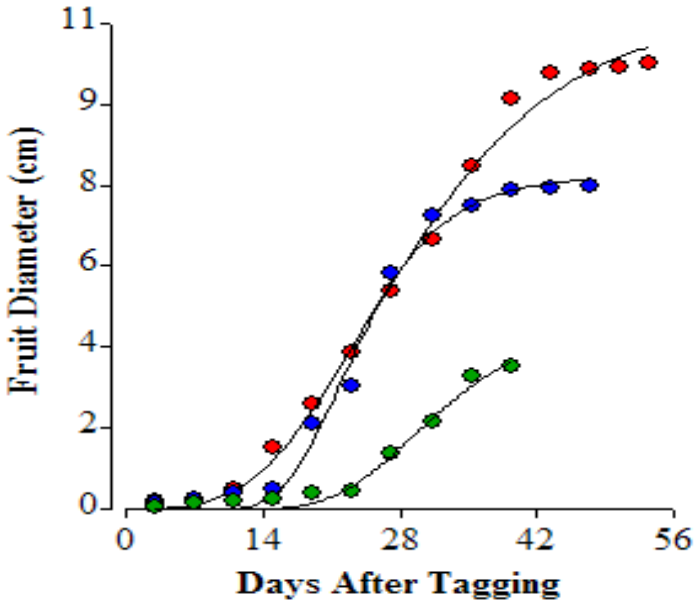

Figure 4-3. Individual fruit growth curves (fruit diameter in cm) over time in 2007, fitted to a three-parameter Gompertz function (●Cohort 1, ●Cohort 2, ●Cohort 3). Each point is a mean of four fruits.

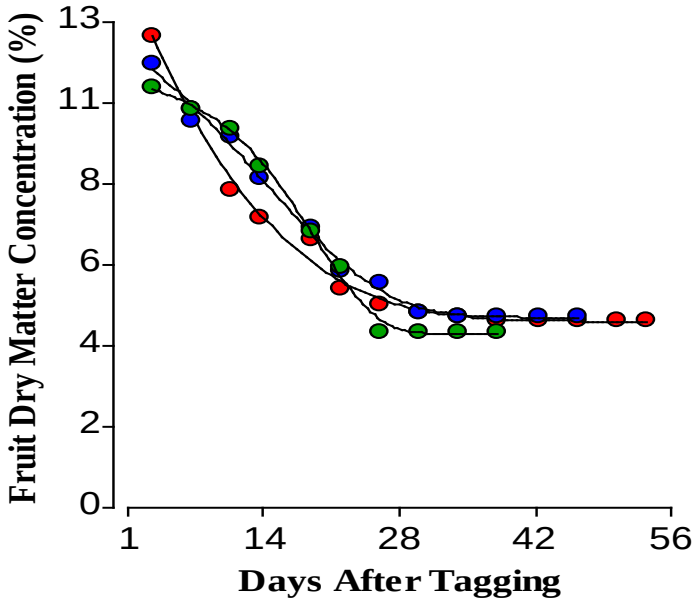

Figure 4-4. Individual fruit growth curves (dry matter concentration) over time in 2007, fitted to a four-parameter Gompertz function with displacement (●Cohort 1, ●Cohort 2, ●Cohort 3). Each point is a mean of four fruits.

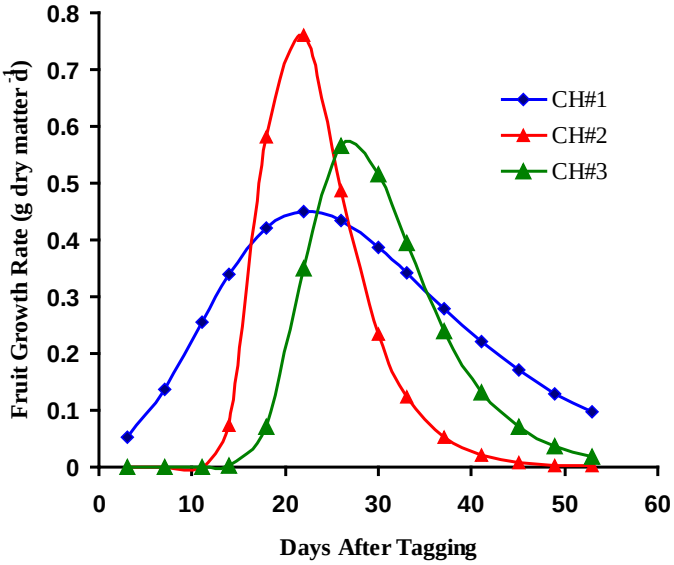

Figure 4-5. Individual fruit growth rate (g dry matter per day) over time, obtained by fitting the 2007 data to a three-parameter Gompertz function and calculating the first derivative of the function.

CHAPTER 5
IMPROVING A TOMATO GROWTH MODEL TO PREDICT FRESH WEIGHT AND SIZE OF INDIVIDUAL FRUITS

Introduction

A number of tomato crop models that simulate fruit dry weight yield have been developed. Tomato growers, however, would be more interested in models that can predict the weekly pattern of yield on a fresh weight basis, including variations in the marketable size. Such a model could assist growers in planning their management and commercialization strategies in order to optimize fruit yield, harvest timing, and fruit quality. These three goals are not easy to attain simultaneously for tomato because the traits that enhance yield are often antagonists of those that increase quality. For example, larger fruits tend to have a lower dry matter concentration (Foolad, 2007). In this sense, simulating the growth of individual fruits may represent an efficient path toward increasing our understanding of the processes involved in the formation of those fruit variables. Modeling of individual fruit behavior over the course of time could be used as a tool to analyze fruit function, as well as to integrate our knowledge about the responses of fruit growth to internal and environmental factors. Researchers study fruit growth in order to answer several important questions in horticulture, such as: what management practice provides the best range of fruit size, shape, yield, and marketable quality? Which fruit cultivar is most suited to a particular growing region? What are the most critical stages during fruit development that may be related to the incidence of physiological defects and disorders? (Opara, 1999).

Horticultural crops like tomato are characterized by a low fruit dry matter concentration that varies between 5 to 6.5 % (De Koning, 2000; Heuvelink, 2005). Photosynthesis-based models simulate dry matter production, but few models have attempted to simulate the dry matter concentration (DMC) or water concentration of fruits. As a consequence, a fixed DMC value is frequently assumed to translate dry weight into fresh weight. However, an error in

predicting fresh weight of more than 25 % may arise when a fixed DMC value is assumed (Marcelis *et al*., 1998). Both plant developmental stages as well as the potential gain in carbon are closely linked to temperature; therefore, to mechanistically simulate fruit growth, it would seem feasible to develop a model that relates carbon accumulation with the physiological or thermal age of the fruits, from anthesis to maturity. Since the amount of accumulated dry matter per fruit will determine how much of the growth will be devoted to fresh mass, it follows that after the crop model predicts the dry mass per fruit and fruit thermal age, an equation for converting the dry weight of fruits to fresh weight must be derived. This approach may be more efficient than trying to track fruit growth over time based on changes in diameter simply because fruit diameter is strongly cultivar dependent, and, therefore, the inherent generic nature of CROPGRO could be lost while trying to parameterize the equations for fruit radii. In addition, early and late set fruits vary in size, which brings up the difficulty associated with predicting the whole dynamics of fruit growth beginning with fruit size. On the other hand, once the fresh mass is simulated, the size of the fruits is relatively simple to model using empirical relationships, which have been established by Bussieres (1993) and verified by Scholberg *et al*. (1997). Based on the conceptual relationships described above, a sub-routine was added in the DSSATV4.5 version of the CROPGRO-Tomato model to predict the dry matter concentration, fresh weight, and radial size of individual fruits over time on a cohort basis. The objective of this chapter is to evaluate the capabilities of this sub-model in predicting the fresh weight and size of individual fruits and to use data from field experiments to calibrate some parameters as well as to assess the quality of the simulations.

Materials and Methods

Field data: The growth data for evaluation were obtained from experiments conducted in field-grown plastic mulched fresh-market tomato plots between April and July of 2006 and

repeated during the next season in 2007. The data from the 2007 season were used to calibrate the genetic parameters, as well as the non-linear adjustment of the equations; therefore, the true independent dataset for the evaluations were collected in 2006.

The experimental area was located at the University of Florida Plant Science Research and Education Unit at Citra, Florida (29◦ 25' N, 82◦ 10' W). The treatment selected for evaluation was well irrigated and well fertilized, so no water or nitrogen stress was present throughout the entire growing season. The soil has been classified as a fine Candler sand and Tavares sand (Buster, 1979; Dukes *et al*. 2005). These soils contain 97% sand-sized particles and have a field water holding capacity of 5.0% to 7.5% by volume in the upper 100 cm of the profile (Carlisle *et al*., 1988; Dukes *et al*., 2005). The cultivar evaluated was Florida 47, a mid- to late-season hybrid whose fruits are deep globe-shaped. Each replicate plot consisted of 15.2 m long rows of 4-wk-old plants established on April 04 in 2006 and April 07 in 2007 in completely mulched fumigated beds. Row spacing was 1.83 m, and plant spacing was 0.45 m, which translated to a plant population of 11,960 plants ha^{-1}. Pre-plant fertilizer applications were 112 kg P2O5 ha^{-1} and 45 kg ha^{-1} of K_2O. Treatments were replicated four times using a randomized complete block design. Water application was based on the calculated crop ET, and N rates were based on IFAS recommendations consisting of 224 kg N ha^{-1}, which was applied with the irrigation water. Irrigation was applied via the drip tape system, and emitters were spaced 20 cm apart. Climatic data, including temperature, solar radiation, rainfall, wind, and humidity were collected by an automatic weather station located within 1 km of the experimental area.

Growth analysis: Periodically (every 14 days), four plants per treatment were destructively measured. Stems, removed leaves (separated into blades and petioles), and picked

fruits were dried in a ventilated oven at 60 ºC for at least one week, and leaf area was measured with a LICOR Model 3100 Area Meter (Lincoln, Nebraska, USA).

Growth analysis of individual fruits: At the time of anthesis, three sets of flowers separated by one week in age were tagged. For each cohort date, at least 60 flowers were tagged in each replicate (modified from Heuvelink, 1995). Beginning 3 days after anthesis and two times per week, two tagged fruits in each plot were randomly sampled at 0800 h in the morning. Therefore, samples were collected at 3, 7, 11, 14, 18, 22, 26, 30, 33, 37, 41, 45, 49, and 53 DAA (days after tagging). During sampling, the fruit diameter was measured, the fresh weight was recorded, and the dry weight was destructively determined.

Total yield: A total of 32 plants were selected for the final yield. At harvest, complete plants (8 per replicate) were harvested separately. The number of fruit was recorded for each replicate and classified according to fruit size. Fruit size designation was in agreement with the United States standards for grades of fresh tomatoes. The fresh weight of fruits was recorded and 1 kg of fruit for each size designation was sampled for dry weight determination. The rest of each harvested plant was chopped and dry weight was determined in order to obtain the fruit harvest index at harvest.

The model: The CROPGRO model used in this study is not yet the official version of the DSSAT software. It has the characteristics of version V4.5, which will be released in 2009 with fresh weight and the genetic files of the updated parameters explained in Chapter 3. The general description was presented in Chapter 3, and more detailed information may be found in the references mentioned therein. In this section, only characteristics of the model related to fruit growth are described. The CROPGRO model explicitly predicts fruit addition and fruit growth rates over time for the cohorts added daily. The number of fruits, seeds, and flowers that are

initiated each day are stored and updated dynamically, allowing us to know not only the number of fruits, seeds, and flowers but also the real time ages of the fruits as well as their physiological ages. This capability of the model is a benefit over other models for which the number of fruits is often an input. As each individual cohort of fruits is added, individual fruits possess their own inherent dry matter accumulation rate based on the genetic potential growth rate and temperature (Boote and Scholberg, 2006). Additionally, a proportion of fruits are allowed to abort based on C availability, N availability, and a water stress variable. The cultivar-specific parameter XFRUIT determines how much of the maximum fraction of the daily available C is partitioned to fruits. The XFRUIT parameter can be equal to 1.0 for totally determinate cultivars and less than 1.0 for semi and indeterminate cultivars. Seeds (the number of seeds per shell) are set inside the shell after a certain period of time (FLSD-FLSH) after shell growth begins. A growth duration (LNGSH) also exists for each shell, as well as for the seeds (SFDUR). The CROPGRO model predicts the physiological or thermal age of each fruit cohort, and fruit shells are divided into age classes. When shells are less than LNGPEG thermal days in age, they are assumed to grow slowly in mass. How slowly they grow depends on a species parameter called SHLAG, which represents a fraction of the rapid shell growth rate. Cohorts are checked by the model to determine if their physiological age is younger than LNGPEG, between LNGPEG and LNGSH, or older than LNGSH thermal days. After fruits are LNGPEG thermal days in age, they grow at a constant rapid rate. This rapid growth continues until fruits are LNGSH thermal days old, after which growth is no longer allowed (Boote *et al*, 2000). In Chapter 3, the species parameter SHLAG was calibrated (approximately 0.1) to allow a slow growth rate during the first two weeks, in agreement with the normal behavior of tomato fruits, which, during that early phase, display intense cell division rather than a high growth in mass (Mapelli *et al*. 1978; Varga and

Bruinsma, 1986). Dorais *et al*. (2001) reported that during the first weeks after anthesis, tomato fruits grow at a rate that is 10 % of the rapid growth rate, and this slow phase continues for 14 to 21 days depending on the cultivar, the position of the fruit (age), and environmental conditions. The ecotype PM06 coefficient was also calibrated as described in Chapter 3. As explained in that chapter in CROPGRO models, this parameter typically has meaning only for peanut. It represents a fraction of the time between first peg and first seed in the pod. If the PMO6 in the ecotype file is equal to 0.0, the first peg and the first pod occur at the same time. If PMO6 is > 0.0, a slow growth phase occurs prior to the reported first pod. In addition, in order to improve the timing of flower and fruit appearance, several other cultivar parameters were also calibrated.

Modeling individual fruit growth: The submodel included in CROPGRO for fresh mass and size simulations begins with the C balance model predicting the dry matter gain per fruit (plus seeds) over calendar time, along with the prediction of the physiological age of the fruits in thermal time. The function that simulates DW is linear (constant potential rate if assimilate is available but reduced if assimilate is deficient). The fruit dry matter concentration (DMC) is then predicted as a function of fruit thermal age (TT in Equation 5-1). Parameters α, β, φ, and TT_{max} in Equation 5-1 were adjusted to the independent experimental data of the 2007 season using nonlinear regression and fitted values will be presented later. These parameters are in some way mechanistic (Scholberg, 1996). The first parameter α represents the difference between the maximum fruit dry matter concentration (DMC_{max}), which occurs at the time of anthesis. For cultivated tomatoes DMC_{max} is approximately 12 to 14 %, and the minimum concentration at maturity (DMC_{min}) is considered to be a constant equal to 5 %. The parameter β depends on environmental conditions, especially solar radiation. Under field conditions, β is considered as fairly stable during the season; however, in the greenhouse, β likely needs to be calibrated

according the prevalent light conditions (Scholberg, 1996). The intercept φ was added to equation 1 to account for the fact that, for fruit growth simulation, the model starts the accumulation of thermal time on a fruit "start" basis (FL-SH days after flowering), but in the experiments, timing started when flowers were tagged. In the model, fruit growth ends when PAGE is > LNGSH (physiological age is greater than length of shell growth). Equation 5-1 accounts for this ending stabilizing the DMC toward the end of growth when fruits reach a reference fruit thermal age (TT_{max} in Equation 5-1). A reference sum of degree days (ºCd) could be used as well. Scholberg (1996), for instance, found that this value corresponded to a sum of 750 ^{o}Cd. In addition, Scholberg and Boote (2006) proposed a maximum thermal age equal to 40 physiological days using 10 ºC as the basal temperature. Adams *et al*. (2001) reported that 812 ^{o}Cd were accumulated by tomato fruits in order to reach maturity, while De Koning (2000) reported 940 ^{o}Cd. The discrepancies are likely related to the base temperature used by each author. Scholberg (1996) used a basal temperature equal to 10 ºC (fruit progression from anthesis to maturity), De Koning used 4 ºC, and the version of the CROPGRO tomato model used in this paper employed a literature-based value equal to 5.7 ºC (see Chapter 3). The physiological age values used to optimize the parameters in Equation 5-1 were calculated by CROPGRO using a basal temperature equal to 5.7 ºC.

$$DMC = DMC_{\min} + \alpha * EXP(\beta * (TT - \phi) / TT_{\max}) \qquad (5\text{-}1)$$

DMC as a function of the thermal age plus the model-predicted dry mass per fruit (DW, g per fruit) permits computation of fresh mass per fruit (FW, g per fruit) according to Equation 5-2.

$$FW = \frac{DW}{DMC} \qquad (5\text{-}2)$$

The relationship between fruit diameter versus fresh mass, as described by Equation 5-3, is used to predict fruit diameter. To obtain parameters γ and η in Equation 5-3, experimental data from the 2007 season were fitted using an exponential function. The fruit shape factor (FS) was 0.95 for round fruits, 0.90 for flat fruits, and 1.05 for oblong fruits (Bussieres, 1993; Scholberg *et al*., 1997).

$$Diam = \gamma * \left(\eta * FW / 4 * FS\right)^{1/3} \quad (5\text{-}3)$$

Genetic parameters calibration: Genetic parameters of the determinate tomato cultivar *Florida 47* were calibrated with the data from 2007 as explained in Chapter 3.

Model validation: Model validation was performed using independent experimental data collected during the spring season in 2006. The root mean square error (RMSE) and the Willmott index (d) were used as evaluation criteria. The RMSE is a measure of the difference between the simulated and observed data (Rinaldi *et al*., 2007). Simulation results are considered excellent when RMSE is lower than 10% of the mean, good if between 10 and 20 %, fair if between 20 and 30%, and poor if values are greater than 30% of the mean (Jamieson *et al*, 1991; Rinaldi *et al*., 2007). The Willmott or d index is useful to evaluate model predictions of a variable over time. To calculate the d value, the numerator is the MSE, and the denominator is related to the variability in the measured and simulated values (Wallach, 2006). The d value varies between 0 and 1, and a value closer to one indicates better performance of the model (Willmott, 1981).

Results and Discussion

Calibration Results (Year 2007)

Genetic parameters: Several genetic parameters were previously calibrated in order to adjust the development, total biomass, and fruit yield for cultivar FL-47 to the experimental data measured for 2007, as presented in Chapter 3. As explained in that chapter some additional

parameters were calibrated to adjust the growth of individual fruits on a cohort basis to the experimental data measured during the 2007 growth season. First, the timing of flower and fruit appearance was adjusted. The cultivar parameter EM-FL (days between plant emergence and flowering) was calibrated to 25 photothermal days in order to improve the prediction for anthesis date. In addition, the model starts to grow fruit after a certain amount of thermal time is accumulated after beginning peg, but in the experiments, flowers were tagged, and time began at flowering. As a consequence, to match the timing between flowers and the start of slow fruit growth, the cultivar coefficient FL-SH (thermal days between flowering and shell growth) was calibrated to a smaller value (3 photothermal days). In the same way, the time between first seed and fruit maturity was also calibrated. In order to improve the initial growth of fruits and seeds, the coefficients PODUR (duration of pod addition) and SFDUR (duration of seed filling) required calibration. In addition, in order to give some priority to shell growth over seed growth, the threshing percentage was slightly decreased (from 9.2 to 8.5 photothermal days). To track the growth of individual cohorts, the species parameter SHLAG was calibrated to a value equal to 0.1 to allow a slow growth rate during the first 2 weeks, in agreement with the observed growth of tomato fruits. Moreover, to set the duration of this slow fruit growth phase, coefficient PM06 (ecotype file) was calibrated to a value of 0.6 for the three cohorts. The criteria for these calibration processes were primarily that the model had to correctly predict the timing of flowering in order to simulate the development and growth over time of three cohorts whose development and growth began at different dates (separated by one week) based on the tagging dates. At the same time, growth and yield at the whole plant level was calibrated as well. For the present chapter all the genetic coefficients (species, cultivar and ecotype parameters) correspond

to those of Chapter 3 against having been solved plant growth, fruit yield and growth of tagged cohorts from 2007 experimental data and no further calibration was done for this chapter.

Fruit dry weight calibration results: The observed and simulated dry weight accumulation in individual fruits from flowers that had been tagged at three stages is presented in Figures 5-1, 5-2, and 5-3 and Table 5-1 for 2007. There was a very good correspondence between the simulated and observed data with regard to cohorts 1 and 2. In these cohorts, the Willmott agreement index (d) was equal to 0.997 and 0.988 for cohorts 1 and 2, respectively. The high d value indicates that the variability in the observations around the mean was very well tracked by the predictions. The average RMSE for both cohorts was low, on average, approximately 0.78 g, which represents an error lower than 6% of the final fruit dry weight for these cohorts. The less satisfactory, although still acceptable, response of the model was observed for cohort 3, which produced a d of 0.96 and RMSE of 0.51g, representing an error of 14% for the final DW of this cohort.

Optimization of Equation 5-1: The CROPGRO model does not use a Gompertz function as we used in Chapter 4 to simulate the growth of individual fruits. Instead, as stated in the Materials and Methods section, CROPGRO predicts a constant genetic potential growth rate (linear phase) after a lag phase of 10% of the genetic potential (Dorais *et al.* 2001). A set of equations (Eq.5-1 to Eq.5-3) is then used to convert the dry matter per fruit to fresh weight and size. Experimental data for the fruit dry matter concentration obtained in 2007 were fit to Equation 5-1 using non-linear regression in order to optimize the parameters of the equation (Figure 5-4). Fitted parameters for the three cohorts are shown in Table 5-2. The model proposed to estimate DMC exhibited a low MAE, indicating good adjustment. All estimated parameters were significant ($p < 0.0001$), indicating that four parameters are needed to explain the model.

The SE of the four estimated parameters was low, which denotes adequate estimation of the parameters, although, comparatively, the TTmax, and especially the intercept φ, parameters seemed to be more uncertain (higher S.E of the estimates compared with α and β). The φ parameter was added to Eq. 5- 1 to account for the fact that fruit growth simulation in the model initiates the accumulation of thermal time (X-axis in Eq. 5-1) on a fruit "start" basis, but in the experiments, timing began when the flowers were tagged.

CROPGRO uses only one equation to predict the DMC of the three cohorts. Therefore, for simulation, the optimized parameters for cohort 1 were used in Equation 5-1 for all cohorts. For cohort 1, the first parameter α was found to be equal to 10.0 and to represent the difference between the maximum fruit dry matter concentration and the minimum concentration at maturity. Parameter β was found to be equal to -7.1. In the model, the fruits terminate their growth when they reach a reference fruit thermal age (TTmax in Eq. 5- 1). This maximal thermal age was solved to be 55 thermal days in the adjustment for cohort 1. For this cohort, the intercept φ was equal to 1.6.

Fruit dry matter concentration calibration results: The observed and simulated dry matter concentration of individual fruits from flowers that had been tagged at three stages are presented in Figures 5-5, 5-6, and 5-7 and Table 5-1 for 2007. Simulated and measured data agreed reasonably well, with RMSEs of 0.3 % and 0.9 % for cohorts 1 and 2, respectively, which represent a model error of 6 % and 18 % for the fruit DMC of cohorts 1and 2 and a higher MSE (1.2 %) for cohort 3, representing an error of 24 % for the fruit DMC. The Willmott index was high (0.996 and 0.97 for cohorts 1 and 2, respectively), but it was lower (0.94) for cohort 3.

Fruit fresh weight calibration results: The observed and simulated fresh weight accumulation in individual fruits from flowers that had been tagged at three stages are presented

in Figures 5-8, 5-9, and 5-10 and Table 5-1 for 2007. A very good correspondence was observed between the simulated and observed data in cohorts 1 and 2. In these cohorts, the Willmott agreement index (d) was equal to 0.99 for both cohorts. The average RMSE for both cohorts was low (15 g), which represents an error of only 5.4 % of the single final fresh fruit weight. Similar to the dry weight prediction, acceptable, though less satisfactory, results were detected for cohort 3, which demonstrated a d value of 0.95 and a higher RMSE (12.9 g), representing an error of 16.7 % for the final fresh weight of fruits in this cohort.

Optimization of Equation 5-3: The relationship between fruit diameter versus fresh mass as described by Eq. 5- 3 is used to predict fruit diameter. Parameters γ and η were optimized for Eq. 5- 3 by fitting the experimental data for fruit diameter measured during 2007. The results are shown in Table 5-2. The MAE of the model was low, indicating a good model. The optimized parameters provided a γ of 20.05 and η equal to 0.02 for the three cohorts. The SE of the estimations was low, indicating that the parameters were adequately estimated. Moreover, both parameters are important for explaining the model ($p < 0.0001$). It appears that the cohort effects were not important for Equation 5-3 because the parameters were similar across cohorts. The fruit shape factor (FS) is 0.95 for round fruits and the Florida 47 cultivar is a round-shaped fruit. Therefore, the expression in the denominator of Equation 5-3 is a constant equal to 3.8.

Fruit size calibration results: The observed and simulated fruit diameter of individual fruits from flowers that had been tagged at three stages are presented in Figures 5-11, 5-12, and 5-13 and Table 5-1 for 2007. Comparisons among cohorts showed that the fruit sizes of cohorts 1 and 2 were very well simulated by the model, with an average RMSE of 0.6 cm for both cohorts, which represents an error of only 6.9 % for fruit diameter in both cohorts. The average d value was 0.99, indicating that the variability in the experiment was well captured by the predictions.

Fruit size simulation for cohort 3 was less satisfactory, with an RMSE of 0.74 cm, representing an error close to 22% for the fruit diameter in this cohort, and a d index (0.95) that was acceptable although much lower than that observed for earlier cohorts.

Validation Results (Year 2006)

Validation of the model was performed using independent experimental data collected during the spring season of 2006.

Fruit dry weight: The observed and simulated dry weight accumulation in individual fruits from flowers that had been tagged at three stages during 2006 is presented in Figures 5-14, 5-15, and 5-16 and Table 5-3. There was a very good correspondence between the simulated and observed data for cohorts 1 and 2. In these cohorts, the Willmott agreement index (d) was equal to 0.99 and 0.97 for cohorts 1 and 2, respectively. The average RMSE for both cohorts was also acceptable (1g) and represents a model error of 13.8 % for the total fruit dry weight in these cohorts. A less satisfactory model response was observed for cohort 3, which exhibited an RMSE of 1.12 g, representing a model error equal to 17% of the final DW in this cohort. The d value obtained for cohort 3 was acceptable (0.96). Upon initial inspection, the delayed growth of cohort 3 was likely a result of the priority exerted by older cohorts and was reasonably simulated by the model. However, the simulated delay was too short, since the measured data showed that cohort 3 resumed growth and entered a phase of fast growth later in the growth period. The opposite was observed in 2007 when the model behaved in an opposite fashion, indicating that the delay was too long for cohort 3. However, those fruits did not attain a high mass, likely because this period of fast growth was too short. Such an effect mostly occurred when the fast phase of growth was terminated in cohorts 1 and 2.

Fruit dry matter concentration: The observed and simulated dry matter concentrations in individual fruits from flowers that had been tagged at three stages are presented in Figures 5-17,

5-18, and 5-19, and Table 5-3 for 2006. The simulated and measured data agreed reasonably well with a RMSE in average for both cohorts of 1.2 % which represent a model error of 16.4% of the mean fruit DMC for these cohorts. The RMSE for cohort 3 was 1.5%, representing a model error of 19 % for the mean DMC in cohort 3. The Willmott index was 0.96 and 0.94 for cohorts 1 and 2, respectively, although it was much lower (0.93) for cohort 3. This last cohort maintained small fruits due to a longer lag phase in growth, as previously noted, which resulted in a higher concentration of dry matter compared with fruits of the same age (calendar days) in the other cohorts. This may explain the higher error observed for this cohort compared with the other two cohorts.

Fruit fresh weight: The observed and simulated fresh weight accumulations in individual fruits from flowers that had been tagged at three stages are presented in Figures 5-20, 5-21, and 5-22 and Table 5-3 for 2006. The simulated and measured data agreed reasonably well with a RMSE in average for both cohorts of 18g, which represents a model error of 9.25% of the fruit fresh weight for these cohorts. The RMSE for cohort 3 (18.3g) represents a model error of 12 % for the single final fresh fruit weight in cohort 3. The Willmott index was 0.99 and 0.98 for cohorts 1 and 2, respectively, but it was lower although still acceptable (0.96) for cohort 3. This last cohort maintained small fruits due to a longer lag phase in growth, as previously noted, resulting in a higher concentration of dry matter as compared to fruits of the same age (calendar days) in the other cohorts. This may explain the higher error observed for this cohort compared with the other two cohorts.

Fruit size: The observed and simulated fruit diameter of individual fruits from flowers that had been tagged at three stages are presented in Figures 5-23, 5-24, and 5-25 and Table 5-3 for 2006. Comparisons among cohorts showed that the fruit size in cohorts 1 and 2 was well

simulated by the model, with an average RMSE of 0.57 cm, representing a model error of 7 % and an average d value equal to 0.985. The fruit size simulation for cohort 3 was less satisfactory, with an RMSE equal to 0.75 cm, which represents a model error of 19 % with regard to fruit diameter. The d value was 0.97. This is not surprising since fruit mass in cohort 3 was also poorly simulated, and because of the dependency of the size equation on FW, the error was propagated as expected.

Ability of the Model to Predict Total Yield and Size Distribution.

Total yield for 2006 and 2007: Overall, the calibration done in Chapter 3 of some additional parameters (SHLAG and PMO6) as well as the reduction of time between first flower and first fruit from 8 to 3 required to predict the growth of individual fruits, did not affect the simulation of total fruit dry weight over time. For years 2006 and 2007, total fruit dry weight over time was in good agreement with measurements for both seasons (Figure 5-26). For years 2006 and 2007, simulated total fresh weight exceeded the measured growth. This is especially seen toward the end of the season (Figure 5-27).

Size Distribution: Figure 5-28 shows the simulated size distribution for year 2007. According to the simulated values, most of the production (50 Mg ha^{-1}) ended in the large category (6.3 to 7.3 cm) which is a good size distribution in the fresh market. The simulated values also explain the overestimation in FW (Figure 5-27) due to the high proportion of fruits in cull class size (smaller than 4.8 cm). Those fruits count for the FW although they do not contribute to the commercial yield of tomato for fresh market. According to the simulation the medium class (5.8 to 6.3 cm) which has commercial value also contributed to total yield. At harvest the model predicted that almost all the marketable yield (47 % of the total) corresponded to the large class (6.3 to 7.3 cm). In addition, 28 % of yield was non marketable cull class. Therefore, simulated number of fruit is not an indicator of high productivity since the model

predicts that the plant is carrying a large number of fruits which contribute to the FW. However, those fruits do not fit the market requirement for fruit size. According to the model, tomato fruits did not reached extra large or maximum large categories likely due an excessive load considering the high contribution of culls class. Figure 5-29 shows simulated and observed size distribution at harvest. The analysis of production by fruit size category indicated that during 2007 40.5%, 19.9% and 20.3% of the observed fresh production corresponded to categories large, extra large and maximum large, respectively. In addition, 11.4%, 5%, and 1.89% corresponded to medium, small and extra small class, respectively. The observed percentage of culls was only 0.6%. The model on the other hand, predicted no fruits in extra large and maximum large categories while most of the yield at harvest was in large and medium classes. For fresh market, the commercial production can be represented by the sum of the categories medium, large, extra large and maximum large. Therefore, during 2007, 92 % of the observed total yield reached commercial size. With the model, the large (46.5%) and medium (18.5%) classes contributed only 65.4% of the total yield in commercial size. However, simulated and observed data agree on the fact that the higher contribution to total marketable yield is from the large class. The simulated and observed percentage also agrees reasonably well through the season (Figure 5-29).

Summary and Conclusion

A simple set of equations was included in CROPGRO to simulate the dry matter concentration, fresh mass, and size of individual fruits over time. Parameters were calibrated from 2007, and the simulated results agreed reasonably well with the measured independent data obtained for 2006. The dynamics of dry matter accumulation, fresh mass changes, and size increases simulated by the model demonstrate its ability to explain and predict fruit growth. Overall, predictions for earlier fruits were more successful than the latest cohort, although even the last cohort generally demonstrated d values above 0.9 and prediction errors lower than 20%.

In addition, the contribution of the latest setting fruits to total fruit yield was almost negligible, and, therefore, the submodel can be used in studies of tomato fruit potential growth as well as for accurate predictions of potential yield and fruit size for tomato without significant errors. In addition, the calibration of the model to simulate the growth of individual fruits did not affect the capabilities of the model to simulate growth at a whole plant level and total fruit yield.

Improvements should be made regarding simulation of the timing at which earlier cohorts truly exert priority in attracting assimilates over the latest fruit set. The model does give priority to older fruits and delays the last cohort, but the delay is not entirely satisfactory. To improve the simulation of priority, rules among cohorts may be especially necessary when plants face severe stress and the priority of older fruits may be accentuated, which affects not only the fruits added last but also the intermediate cohorts. In addition, more indeterminate cultivars for which vegetative growth continues during reproductive growth may increase the sink competition for assimilates in plants in response to stress, reducing the accuracy of the predictions. In general, CROPGRO deals with stress by allowing later-set fruits to grow more slowly to a point at which abortion of fruits occurs if the assimilate availability is dramatically reduced. This approach needs to be tested for confirmation and is examined further in the following chapters.

The size distribution simulated by the model had reasonable agreement with observations for the large marketable class size that contributed most to the commercial yield of tomato in our experiment. There was also good agreement for the medium category. However, the model failed in simulating fruits in the extra large and maximum large sizes. Therefore, further research needs to be done to optimize the simulation of size distribution. Determinacy and ability of the model to add late set fruits needs to be tested as the model predicted more late-set culls than were observed. Still the model was able to produce reasonable outputs showing size distribution over

time, a fact that makes CROPGRO-tomato model a tool with a high potential for practical applications.

Table 5-1. Observed vs. CROPGRO simulated final dry weight, fresh weight, dry matter concentration and fruit size of individual tomato fruits, tagged at three different dates. Observed data came from calibration experiment conducted at Gainesville, Fl during spring in 2007.

Cohort #	Observed	Simulated	RMSE	Willmott index (d)
	DW g fruit $^{-1}$	DW g fruit $^{-1}$		
1	13.6	12.98	0.58	0.99
2	9.1	10.00	0.98	0.98
3	3.6	3.55	0.5 1	0.96
	Fruit DMC (%)	Fruit DMC (%)		
1	5.00	5.0	0.3	0.99
2	4.98	5.0	0.9	0.97
3	4.85	5.1	1.2	0.94
	FW g fruit $^{-1}$	FW g fruit $^{-1}$		
1	279	259	13	0.99
2	172	198	17	0.99
3	72	70	12	0.86
	Fruit diameter (cm)	Fruit diameter (cm)		
1	10.4	10.50	0.20	0.99
2	7.5	7.96	0.77	0.93
3	3.3	2.80	0.74	0.95

Table 5-2. Estimated coefficients solved by fitting data of the experiment 2007 to equation 1 to predict fruit DMC over time for the three cohorts and to equation 3 to predict fruit diameter, (Infostat software).

Parameter	Model DMC (%) = $(5+\alpha*EXP(\beta*(TT-\varphi)/TT_{max})$ MAE = 0.03 (average for the three cohorts)					
	Cohort # 1	S.E	Cohort # 2	S.E	Cohort # 3	S.E
α	10.06	0.60	11.35	0.19	12.71	0.21
β	- 7.10	0.38	-6.80	0.33	-6.03	0.76
φ	1.60	0.21	2.20	1.19	5.83	4.10
TTmax	55.00	0.79	55.00	0.98	55.00	1.61
Parameter	Model Fruit Diameter (cm) = γ *(η*(FW/3.8))^1/3 MAE=0.11 (average for the three cohorts)					
	Cohort # 1	S.E	Cohort # 2	S.E	Cohort # 3	S.E
γ	20.05	0.19	20.07	0.33	20.81	0.160
η	0.020	0.0012	0.021	0.006	0.023	0.092

Table 5-3. Observed vs. CROPGRO simulated dry weight, fresh weight, dry matter concentration and fruit size of individual tomato fruits, tagged at three different dates. Observed data came from validation experiment conducted at Gainesville, Fl during spring in 2006.

Cohort #	Observed	Simulated	RMSE	Willmott index (d)
	DW g fruit $^{-1}$	DW g fruit $^{-1}$		
1	10.8	10.58	0.75	0.99
2	7.9	10.11	1.4 0	0.98
3	6.3	8.17	1.12	0.97
	Fruit DMC (%)	Fruit DMC (%)		
1	4.8	5.0	1.20	0.93
2	4.7	5.0	1.30	0.94
3	4.9	5.1	1.50	0.92
	FW g fruit $^{-1}$	FW g fruit $^{-1}$		
1	224	210	19.0	0.99
2	173	201	17.6	0.99
3	154	161	18.0	0.98
	Fruit diameter (cm)	Fruit diameter (cm)		
1	9.0	8.5	0.77	0.98
2	7.2	8.1	0.52	0.99
3	3.9	5.6	0.78	0.97

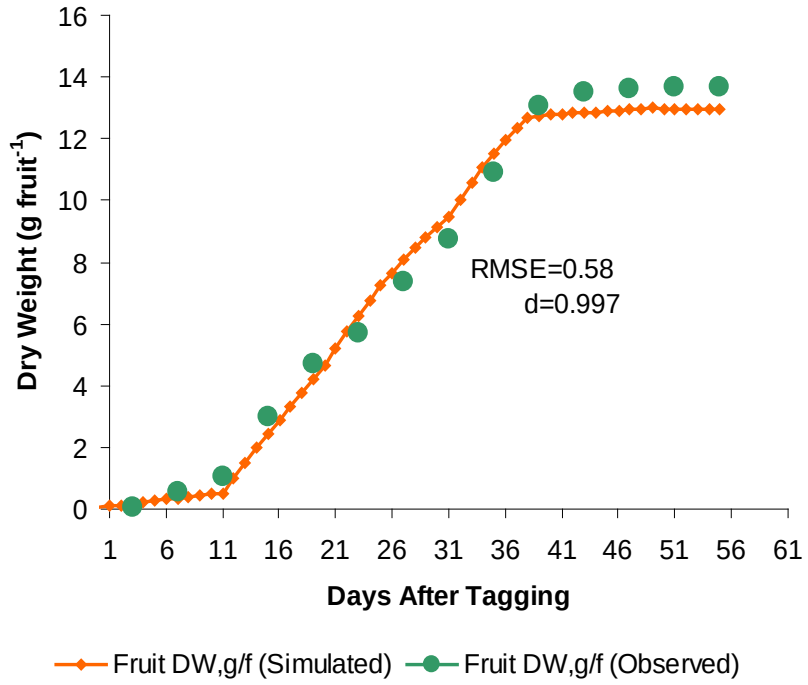

Figure 5-1. Predicted vs. observed dry weight of individual fruits of cohort # 1 in Gainesville Fl, during spring 2007 (each point is a mean of four fruits).

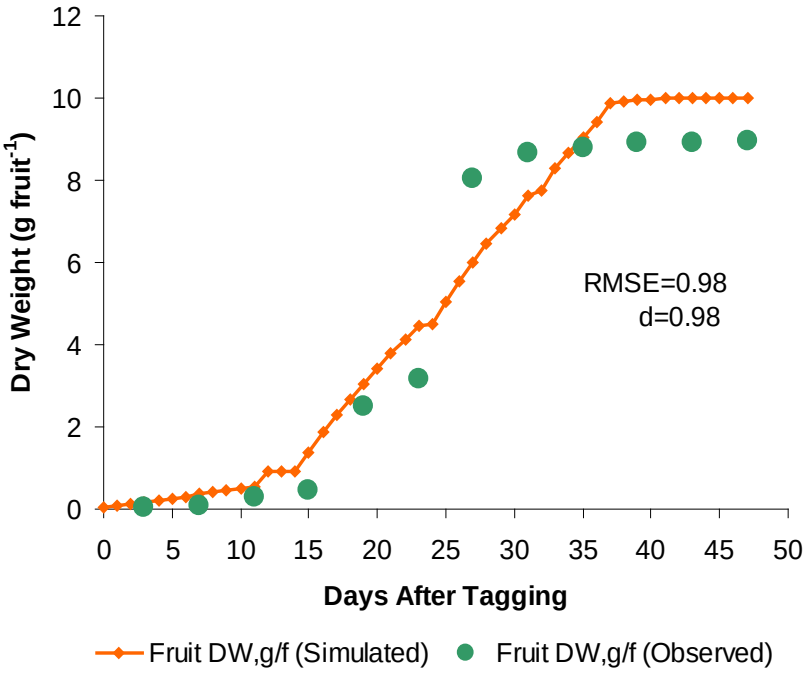

Figure 5-2. Predicted vs. observed dry weight of individual fruits of cohort # 2 in Gainesville Fl, during spring 2007 (each point is a mean of four fruits).

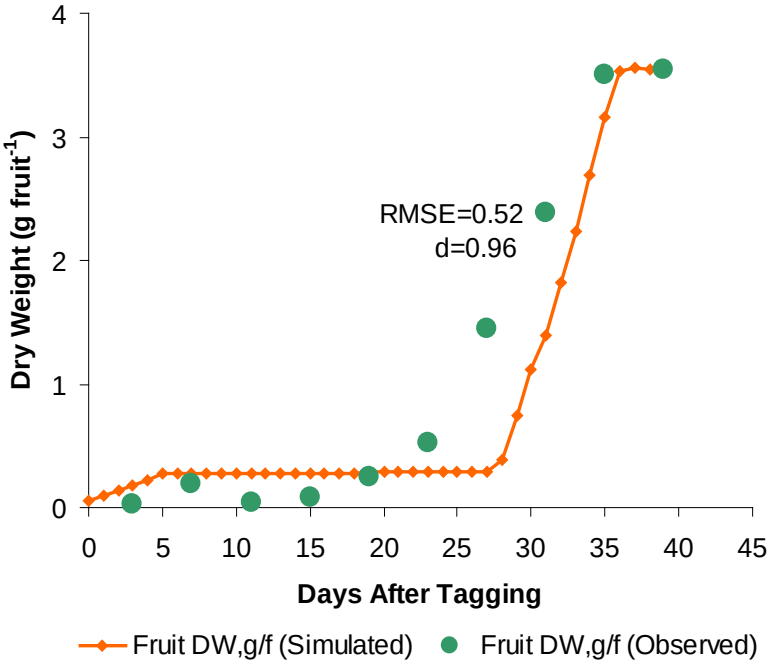

Figure 5-3. Predicted vs. observed dry weight of individual fruits of cohort # 3 in Gainesville Fl during spring 2007 (each point is a mean of four fruits).

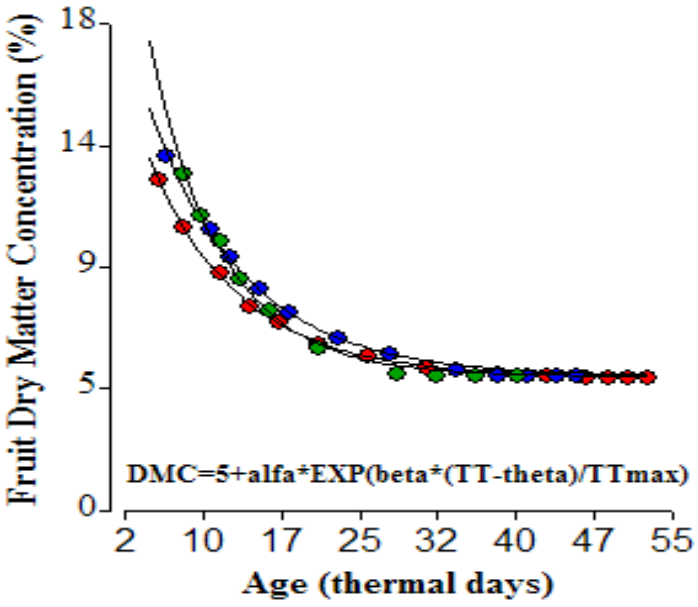

Figure 5-4. Fruit dry matter concentration over time fitted to a four parameter CROPGRO function in 2007 (●Cohort #1, ●Cohort #2, ●Cohort #3), each point is a mean of four fruits.

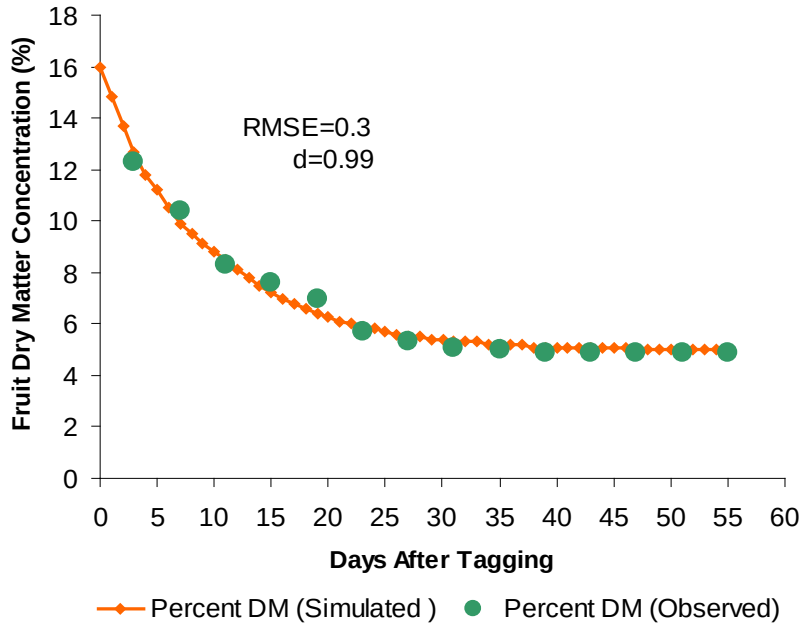

Figure 5-5. Predicted vs. observed dry matter concentration of individual fruits, cohort # 1 (each point is a mean of four fruits) in Gainesville Fl, during spring 2007.

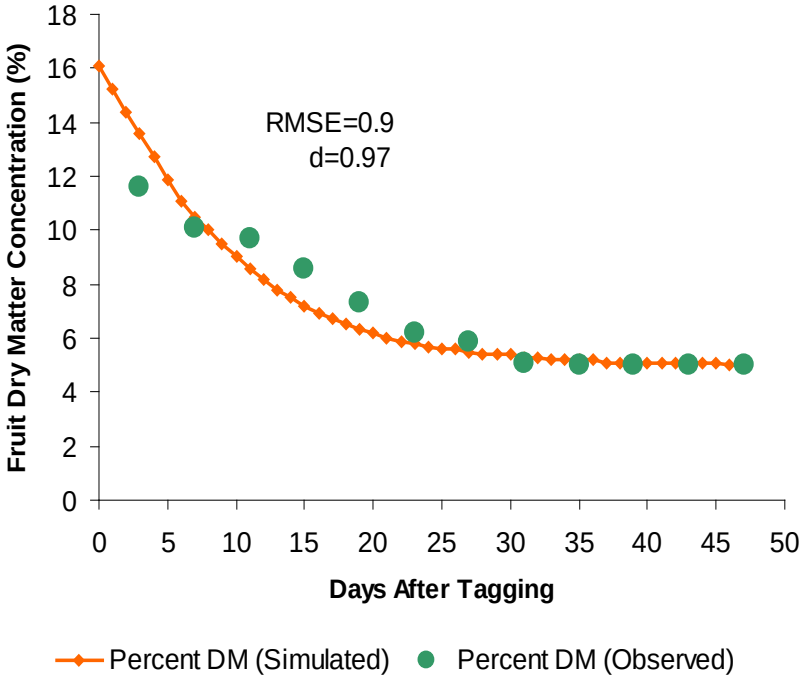

Figure 5-6. Predicted vs. observed dry matter concentration of individual fruits of cohort # 2 in Gainesville Fl, during spring 2007 (each point is a mean of four fruits).

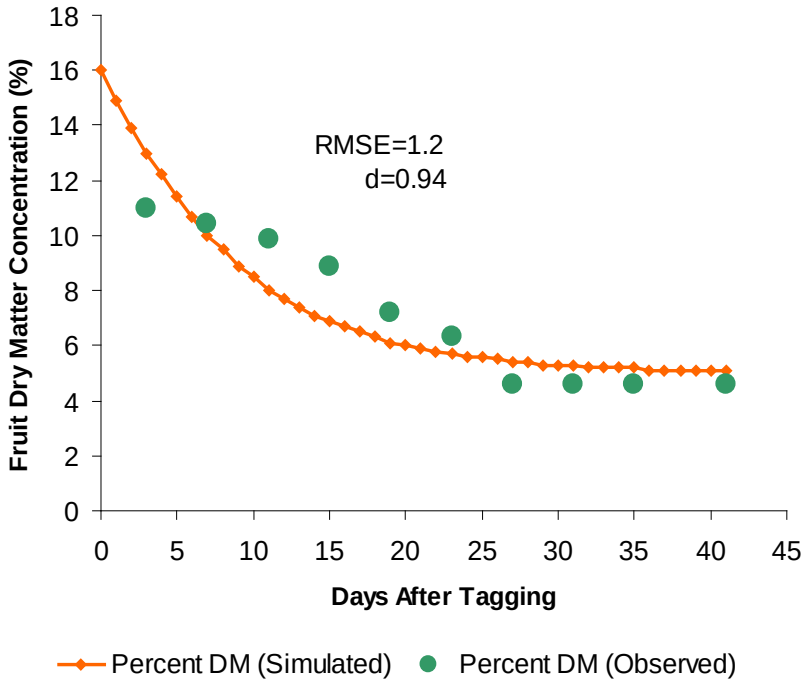

Figure 5-7. Predicted vs. observed dry matter concentration of individual fruits of cohort # 3 in Gainesville Fl, during spring 2007 (each point is a mean of four fruits).

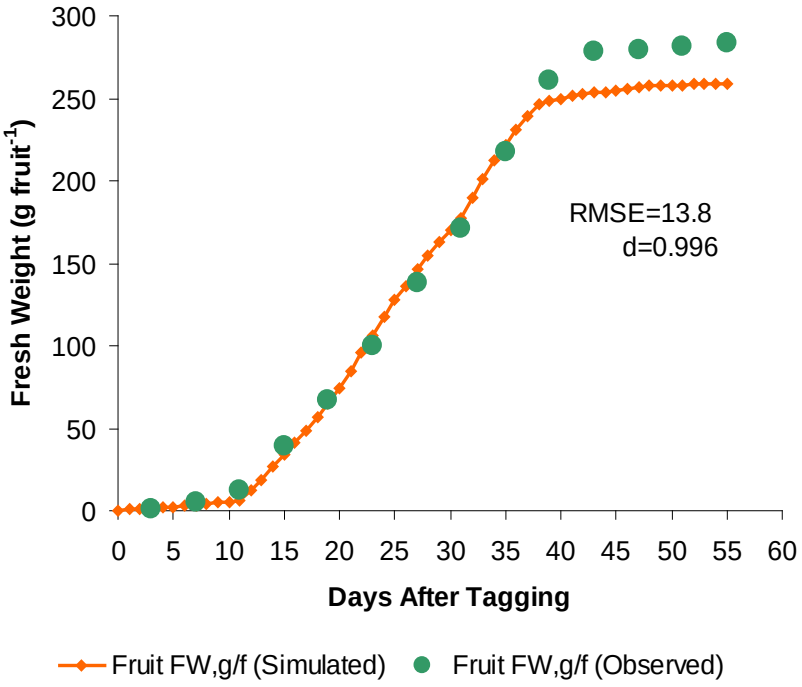

Figure 5-8. Predicted vs. observed fresh weight of individual fruits of cohort # 1 in Gainesville Fl, during spring 2007 (each point is a mean of four fruits).

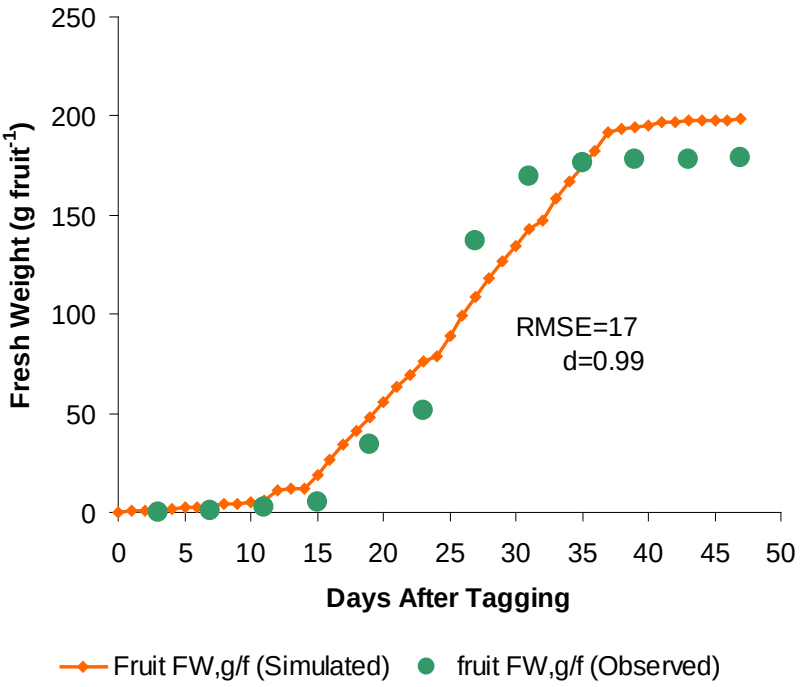

Figure 5-9. Predicted vs. observed fresh weight of individual fruits of cohort # 2 in Gainesville Fl, during spring 2007 (each point is a mean of four fruits).

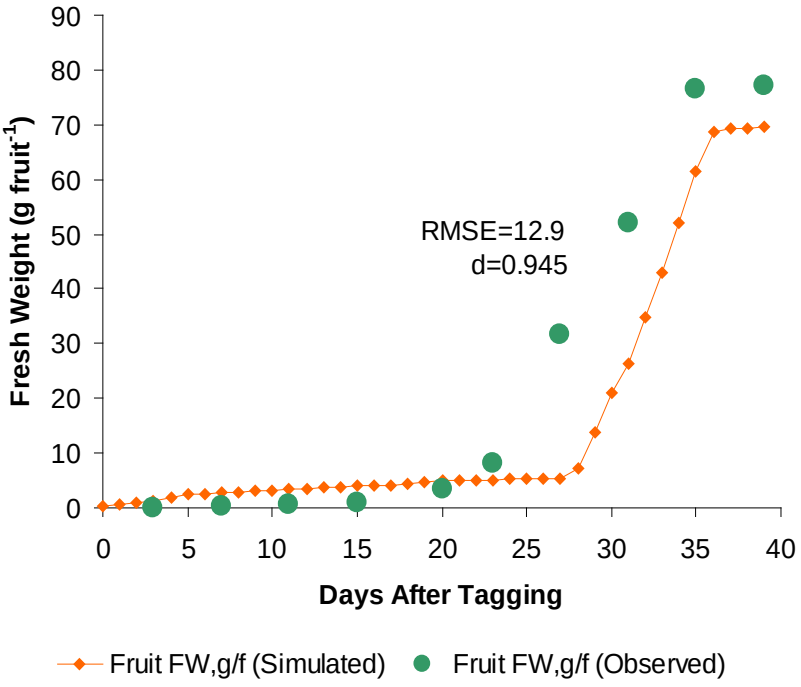

Figure 5-10. Predicted vs. observed fresh weight of individual fruits of cohort # 3 in Gainesville Fl, during spring 2007 (each point is a mean of four fruits).

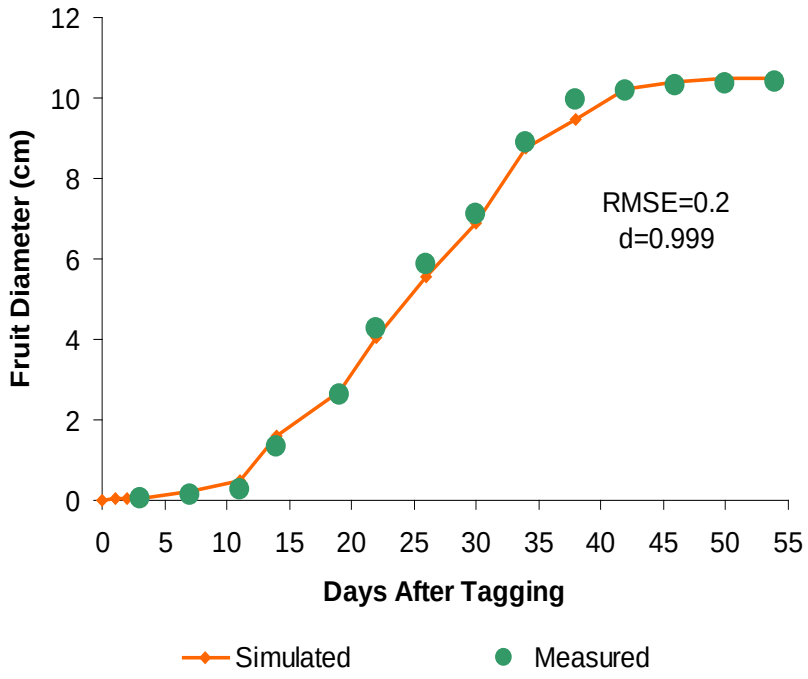

Figure 5-11. Predicted vs. observed fruit diameter of individual fruits cohort # 1 in Gainesville Fl, during spring 2007 (each point is a mean of four fruits).

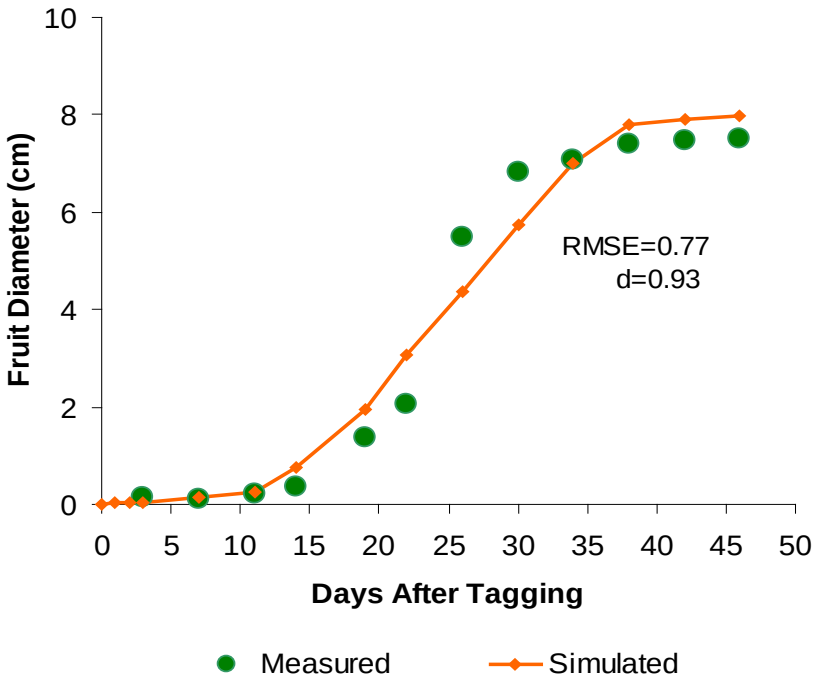

Figure 5-12. Predicted vs. observed fruit diameter of individual fruits cohort # 2 in Gainesville Fl, during spring 2007 (each point is a mean of four fruits).

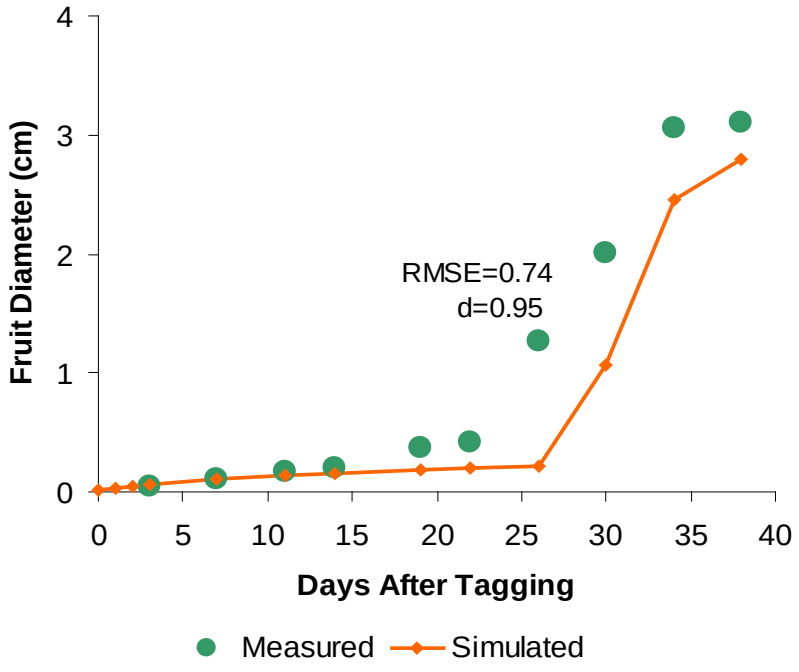

Figure 5-13. Predicted vs. observed fruit diameter of individual fruits cohort # 3 in Gainesville Fl, during spring 2007 (each point is a mean of four fruits).

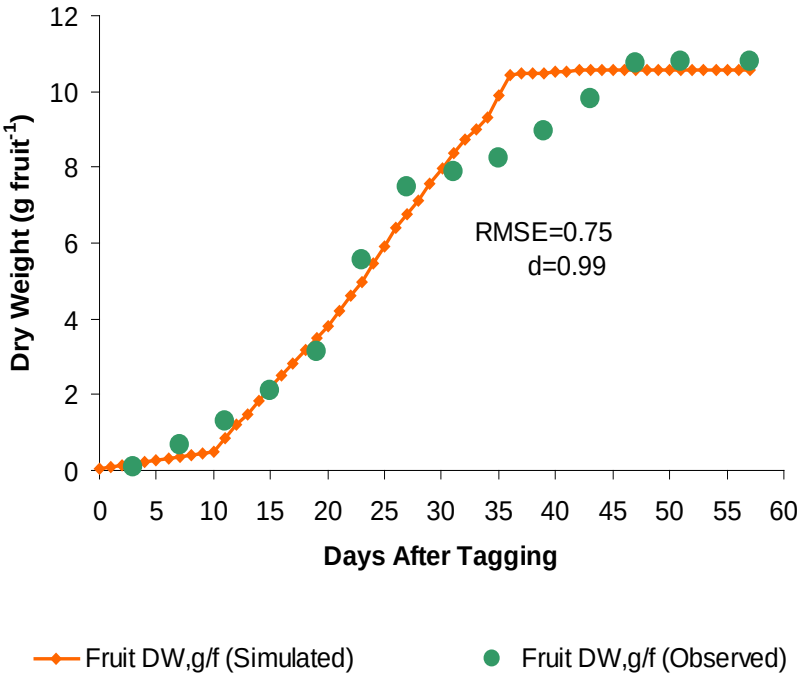

Figure 5-14. Predicted vs. observed dry weight of individual fruits of cohort # 1 in Gainesville Fl, during spring 2006 (each point is a mean of four fruits).

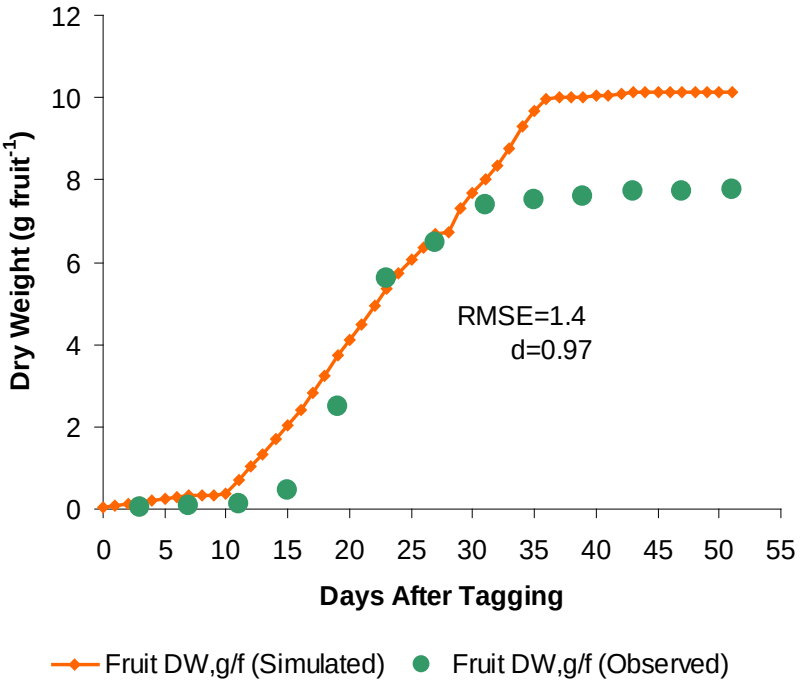

Figure 5-15. Predicted vs. observed dry weight of individual fruits of cohort # 2 in Gainesville Fl, during spring 2006 (each point is a mean of four fruits).

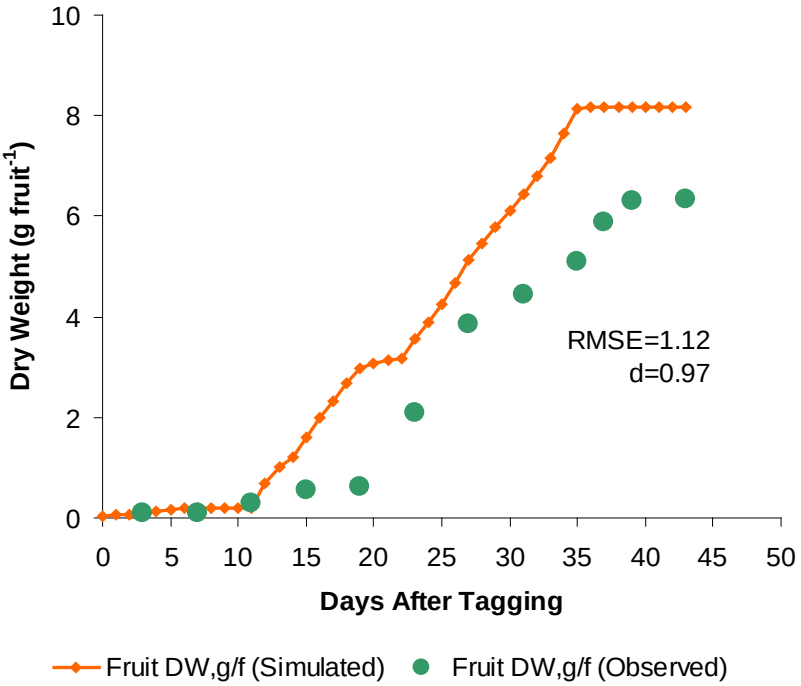

Figure 5-16. Predicted vs. observed dry weight of individual fruits of cohort # 3 in Gainesville Fl, during spring 2006 (each point is a mean of four fruits).

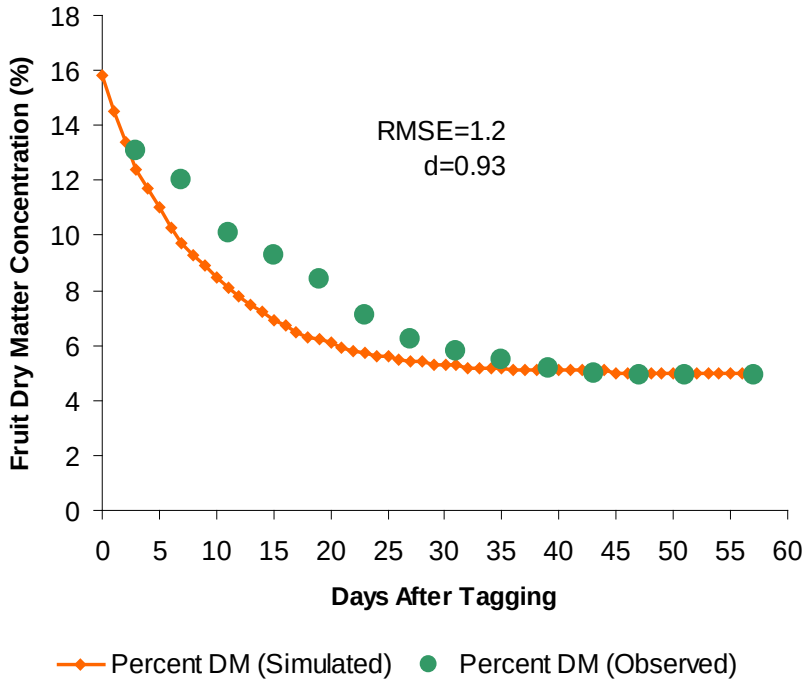

Figure 5-17. Predicted vs. observed dry matter concentration of individual fruits of cohort # 1 in Gainesville Fl, during spring 2006 (each point is a mean of four fruits).

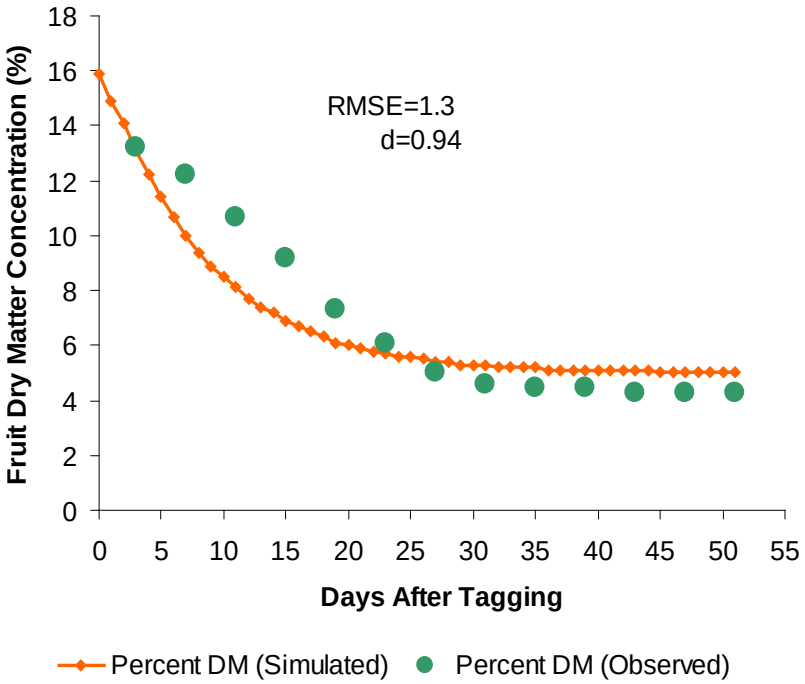

Figure 5-18. Predicted vs. observed dry matter concentration of individual fruits of cohort # 2 in Gainesville Fl, during spring 2006 (each point is a mean of four fruits.

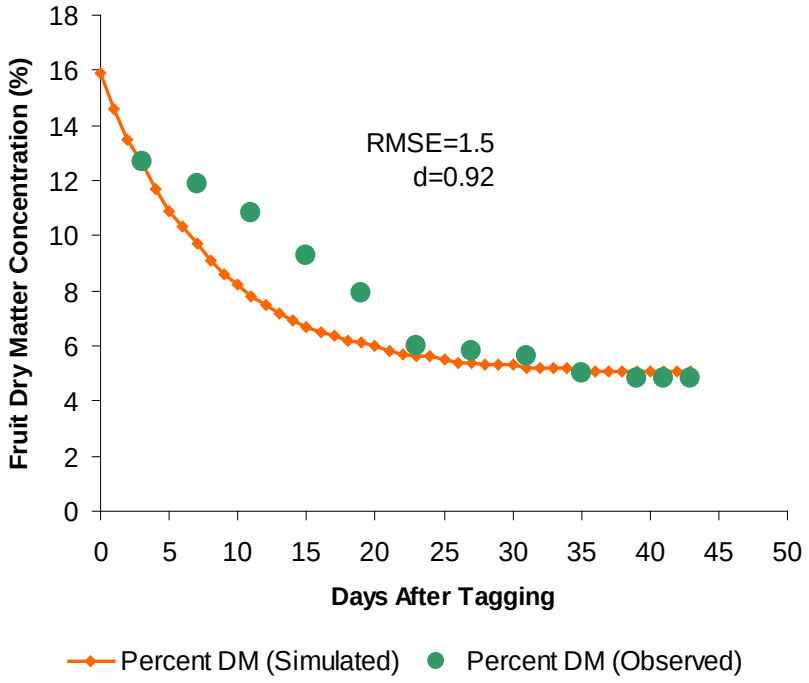

Figure 5-19. Predicted vs. observed dry matter concentration of individual fruits of cohort # 3 in Gainesville Fl, during spring 2006 (each point is a mean of four fruits).

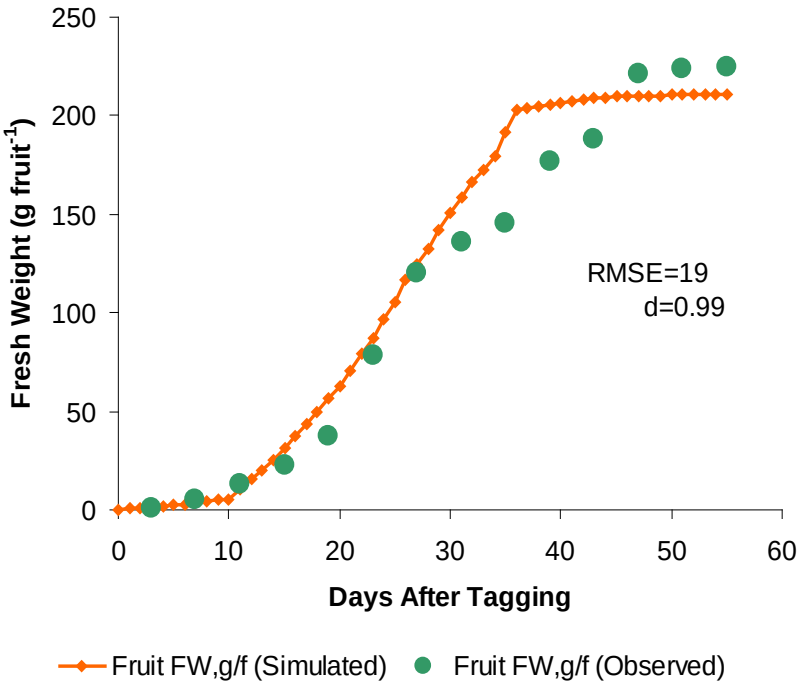

Figure 5-20. Predicted vs. observed fresh weight of individual fruits of cohort #1 in Gainesville Fl, during spring 2006 (each point is a mean of four fruits).

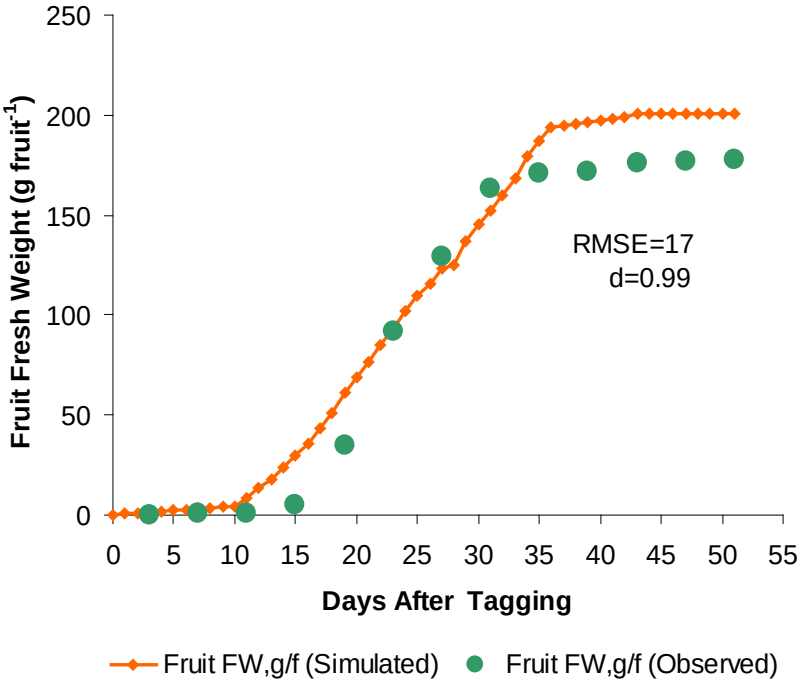

Figure 5-21. Predicted vs. observed fresh weight of individual fruits of cohort #2 in Gainesville Fl, during spring 2006 (each point is a mean of four fruits).

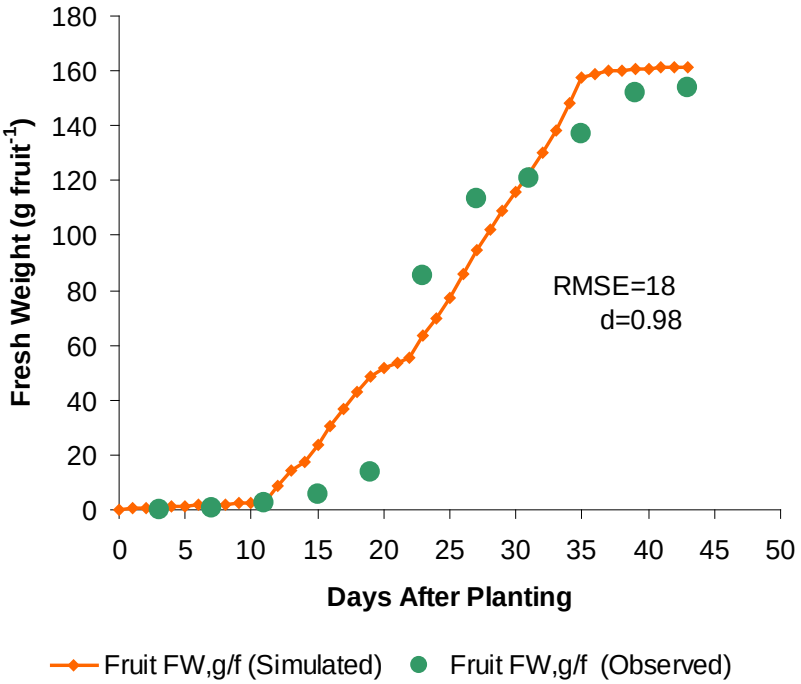

Figure 5-22. Predicted vs. observed fresh weight of individual fruits of cohort #3 in Gainesville Fl, during spring 2006 (each point is a mean of four fruits).

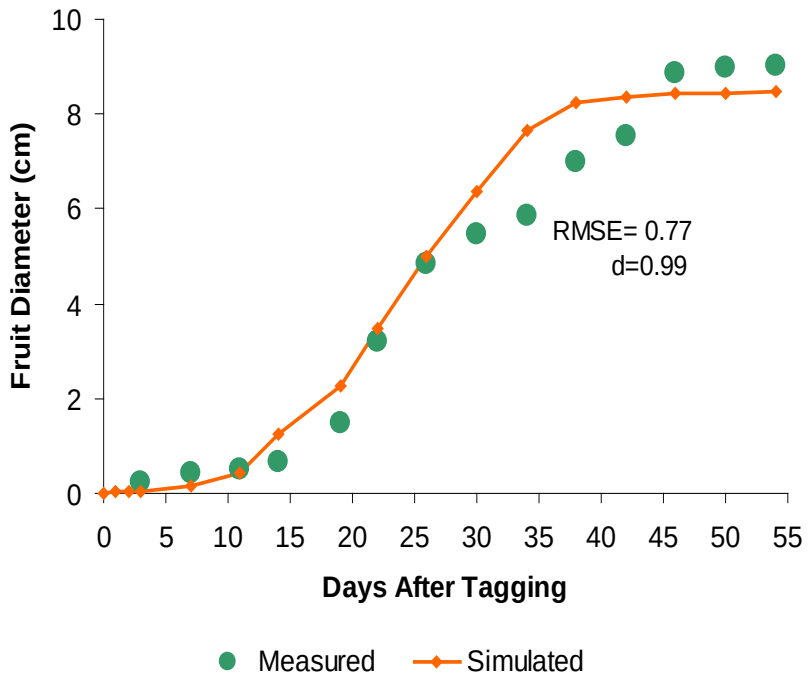

Figure 5-23. Predicted vs. observed fruit diameter of individual fruits cohort # 1 in Gainesville Fl, during spring 2006 (each point is a mean of four fruits).

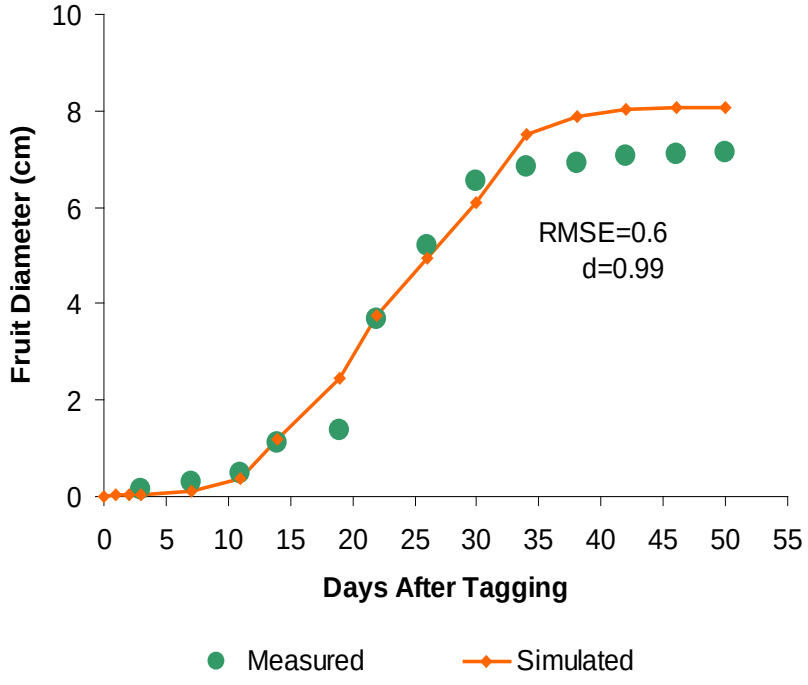

Figure 5-24. Predicted vs. observed fruit diameter of individual fruits cohort # 2 in Gainesville Fl, during spring 2006 (each point is a mean of four fruits).

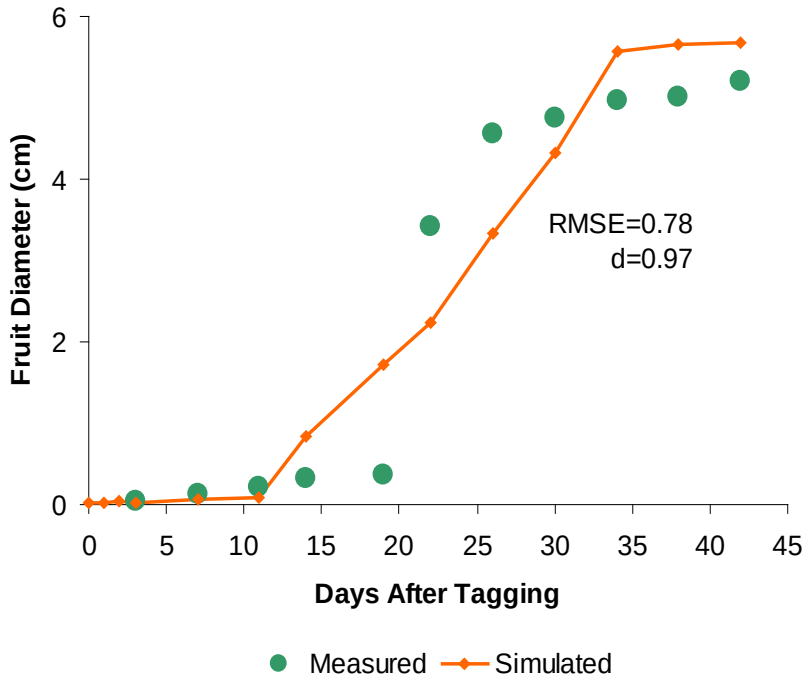

Figure 5-25. Predicted vs. observed fruit diameter of individual fruits cohort # 3 in Gainesville Fl, during spring 2006 (each point is a mean of four fruits).

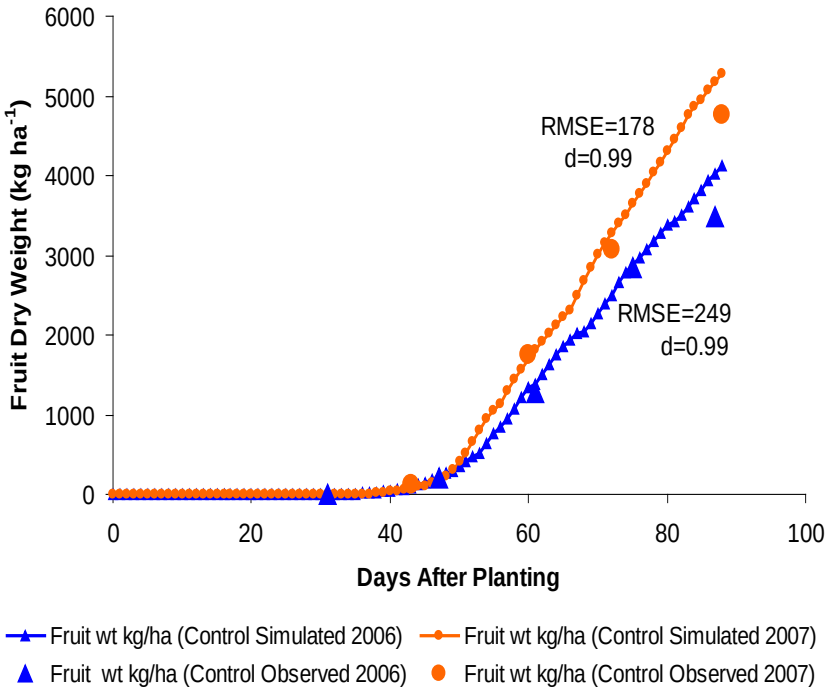

Figure 5-26. Predicted vs. observed total fruit dry weight in Gainesville Fl, during spring 2006 and 2007.

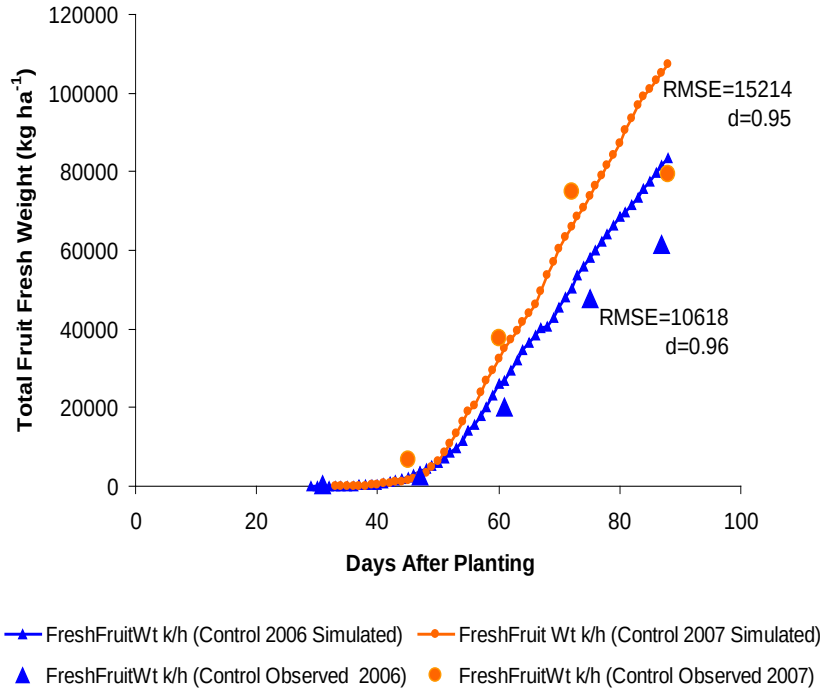

Figure 5-27. Predicted vs. observed total fruit fresh weight in Gainesville Fl, during spring 2006 and 2007.

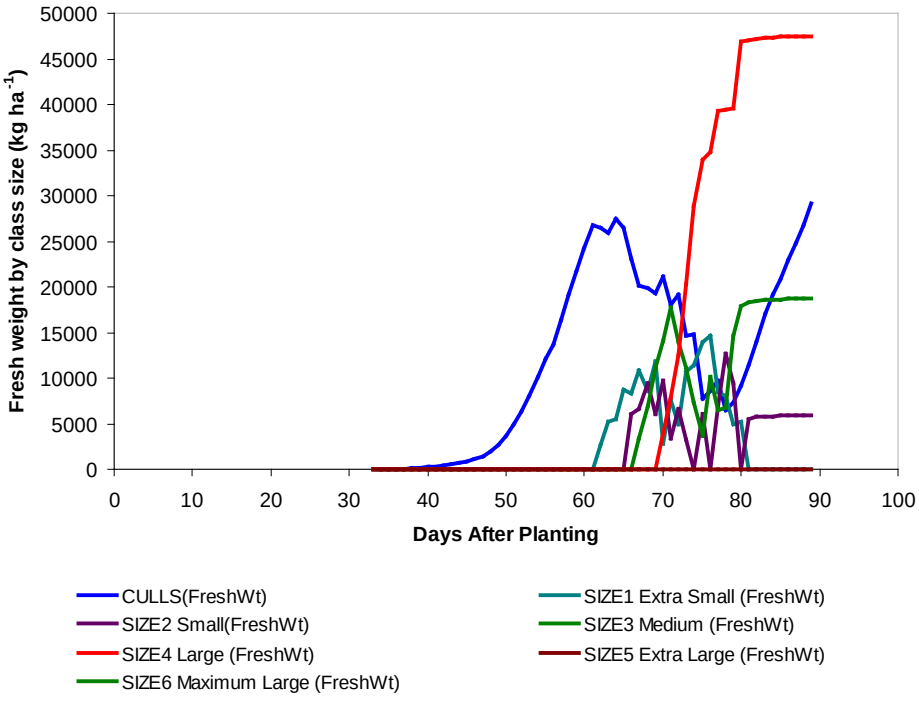

Figure 5-28. Prediction over time of fruit fresh weight as contributed by each marketable size class of tomatoes in Gainesville Fl, during spring 2007.

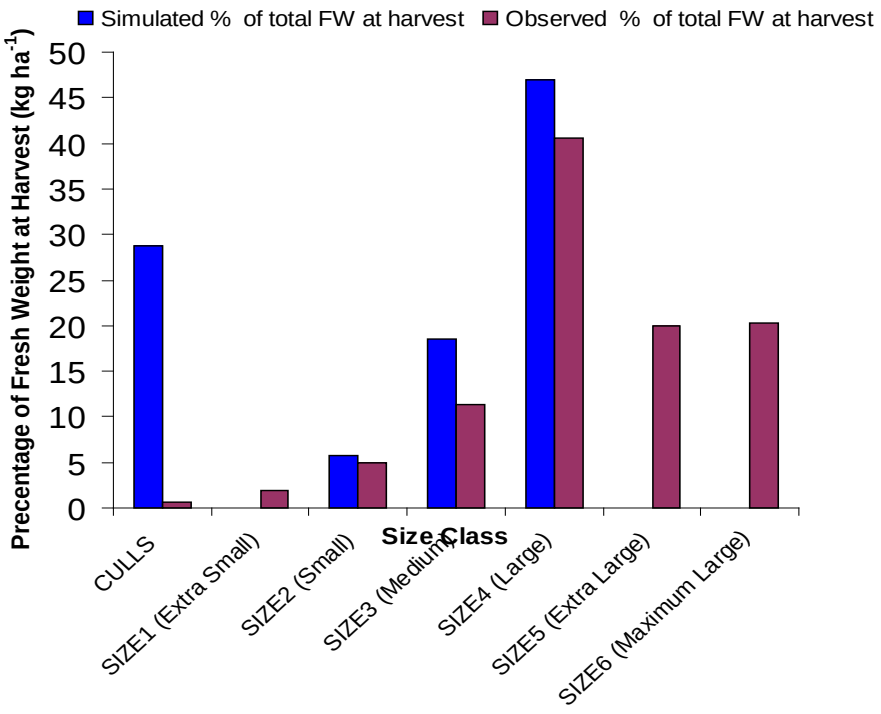

Figure 5-29. Predicted vs. observed total tomato fruit fresh weight contributed by each marketable size class at harvest in Gainesville Fl, during spring of 2007.

CHAPTER 6
EFFECTS OF WATER AND NITROGEN STRESS ON FRUIT GROWTH AND TOMATO YIELD

Introduction

Water and nitrogen (N) fertilizer are important factors for achieving a high tomato yield (Erdal *et al.*, 2006). Several studies have shown that the growth and yield of tomatoes are reduced when water and N are deficient (Sweeney *et al.*, 1987; Scholberg 1996; Scholberg *et al.;* 2000). Tomato crops are highly responsive to N fertilizer. This is particularly true when it is grown in sandy, low organic matter soils (Taber, 2005; *Erdal et al.*, 2006). During the growing season, tomatoes can uptake 150 to 300 kg ha^{-1} of N (Larouche *et al.*, 1989). During rapid growth, N uptake rates may exceed 4.3 kg ha^{-1} d^{-1} (Dumas, 1990; Rinaldi *et al.*, 2007). According to Warner *et al.* (2004), the N requirements of tomatoes are higher during vegetative rather than reproductive growth. Their results agree with Scholberg (1996) and Scholberg *et al.* (2000), who showed that severe N stress significantly reduced leaf area index (LAI), biomass and fruit yield compared to well-fertilized plants. The concentration of N in vegetative organs, such as leaves and stems, was reduced under N stress. The fruits maintained a relatively stable N concentration. Under N stress, the radiation use efficiency (RUE) was reduced by about 30%. Scholberg *et al.* (2000) related this reduction to a lower specific leaf N. This in turn affected the photosynthesis rate. The leaf photosynthesis rate, like RUE, was only reduced by 30% compared to control plants. This occurred because the leaves were thicker (high SLW) under N stress. However, the leaf N concentration was dramatically reduced (40 to 15 mg g^{-1}). High production, sufficiently fertilized plants should have 3% to 4% N in their leaves (Lorenz and Tyler, 1983; Mills and Jones, 1987; Hochmuth, 1994). Optimum N must be available early. Deficiency symptoms do not appear until the leaf N concentration drops below 2%, a level at which the yield is reduced (Taber, 2005). Huett (1986) and Huett and Dettmann (1988) reported an

increased yield of semi-determinate tomatoes in response to increasing N. This finding was associated with higher ratios of dry fruit matter to total plant dry matter. In tomato crops where the fruits are the dominant sinks, the N level influences the dry matter in the fruits. Hebbar *et al*. (2004) reported a 33% higher fruit yield in N fertigated tomatoes compared to plants with low N treatment. They attributed this yield increment to higher LAI, number of fruit and dry matter production.

A water deficit occurs in plants when the rate of transpiration exceeds absorption. Deficiency is accompanied by inhibition of growth and development (Wolf and Rudich, 1988). Cleary *et al*. (1996) considered tomatoes to be in the group of plants having a low tolerance to water stress. They suggested that a water potential in the plant leaves in the range of -0.1 to -0.5 MPa indicates a good supply of water to the plants.

More than 90% of a ripe tomato fruit is water and only 5% to 8% of the weight is dry matter (Davies and Hobson, 1981). Consequently, factors affecting water accumulation may determine the size and quality of the tomato fruit (Grange *et al*. 1987). Ho *et al*. (1987) estimated that the water supply to tomato fruits is predominantly supplied via the phloem. On average, 80% to 85% of the water supply to tomato fruits occurs via this pathway (Ho *et al*., 1987; Guichard *et al*., 2005). The studies on water stress have focused on fruit size, which is largely a measure of the fresh weight (Berman and Dejong, 1996). Research on tomatoes suggests that water stress limits fleshy fruit water accumulation but does not affect carbon partitioning to the fruits (Ehret and Ho, 1986). Scholberg (1996) evaluated the effects of water supply on tomato fruit grown under field conditions. His experimental data showed that fresh fruit weight was more strongly affected by water stress than dry fruit weight. The decrease in yield under stress was attributed to smaller and fewer fruits compared with the controls. In

addition, Garcia *et al*. (2004) found that one important response of tomato plants to early season water stress was a significant reduction in the number of floral buds. There was also a delay in the appearance of floral buds. Ehret and Ho (1986), Mitchell *et al.* (1991), and van Ieperen *et al.* (2005) showed that water stress during the growth of tomatoes reduced the fruit size by 30%. In addition, many investigations have reported that irrigating at a rate of 120 or 140% of evapotranspirative demand increased the fresh weight yield in tomato crops (Ortega Farias, 2003).

Wolf and Rudich (1988) studied the effects of water stress on dry weight accumulation and the growth of individual fruits. The rate of dry matter accumulation was higher in early fruits than late fruits. Dry matter was unaffected by the water regime. Water stress, however, shortened the duration of fruit growth and accelerated the ripening. Under water stress (-80 kPa of water tension in soil compared with -20 kPa in the control treatment), the fruit from the first week of flowering contributed more than 40% to the final dry weight yield.

The effect of N and water stress on the yield and growth of tomatoes has been well studied (Nyabundi and Hsiao, 1989; Scholberg, 1996, Garcia *et al*, 2004, Hebbar *et al*., 2004). However, little information is available about the effect on the rate of growth of individual fruits. Therefore, the objective of this study was to investigate the fresh and dry weight accumulation of individual tomato fruits under water and nitrogen limitations. The results should increase our understanding of the dynamics of tomato fruit growth under stress. Such information may be used to improve the CROPGRO tomato model to simulate the growth of fruit when water and N become limiting factors.

Materials and Methods

Four week old tomato seedlings (cv. *Florida 47*) were transplanted to the field on April 10, 2007. The experimental area was located at the University of Florida Plant Science Research and

Education Unit in Citra, Florida (29◦ 25’ N, 82◦ 10’ W). The s oil is classified as a fine Candler sand and Tavares sand (Buster, 1979; Dukes *et al.* 2005). These soils contain 97% sand-sized particles. The soil has a field water-holding capacity of 5.0% to 7.5% by volume in the upper 100 cm of the profile (Carlisle *et al*., 1988; Dukes *et al*., 2005). The plants were grown in open fields on plastic, mulched and fumigated beds with 0.45 m spacing in a row and 1.83 m between the rows. Cultural and sanitation management were done as needed according to commercial practices. Pre-plant fertilizer applications were 112 kg P_2O_5 ha^{-1} and 45 kg ha^{-1} of K_2O. Irrigation was applied with a drip tape system and emitters were spaced 20 cm apart. Climatic data, including temperature, solar radiation, wind speed and relative humidity was collected by an automatic weather station located within 1 km of the experimental area.

Treatments: The experiment was set up as a completely randomized block design. Three blocks of four rows (replicates) were selected. Four rows (replicates) received the control treatment (CT), which consisted of plants well irrigated and fertilized during the whole cycle. Water was supplied according to calculated daily crop evapotranspiration (Et). Nitrogen was applied following IFAS recommendations (224 kg N ha^{-1}) along with the irrigation water. Four other rows (replicates) received the water stress treatment (WS). The water stress was imposed by completely withholding irrigation for several days during the experiment. The duration of the water withholding was variable and recorded. The water stressed plants were re-watered when severe leaf wilting was observed and the wilting symptoms persisted during the night (Rahman *et al*., 1999). Periods of water withholding were repeated four times during this experimental treatment. The N fertilization remained the same as in the control. Another four rows (replicates) received the nitrogen stress treatment (NS). In these plants, nitrogen applications were

completely suspended two weeks after transplanting. The plants remained fully irrigated like the control treatment.

Measurements: Soil water content measurements were made using time domain reflectometry (TDRs) probes. Probes were buried at 20 and 40 cm in the beds and 5 cm away from the drip tube. The readings were averaged every 20 minutes for each day and stored in a data logger (CR10X, Campbell Sci. Logan UT). Leaf water potential was measured with a Scholander pressure chamber technique according to Tyree and Hammel (1972). Measurements were taken on two leaves per plant and two plants per replicate at midday (from 12h to 13h). Determinations were made at 3-day intervals during the experiment. After fruit setting was complete, net leaf photosynthesis, leaf conductance and transpiration flux were measured on two leaves per plant and two plants per replicate from a canopy that was well-exposed to sun (above 1000 µmol m^{-2} s^{-1}). Measurements were taken on 06/05, 06/08, 06/11, 06/14, 06/18, 06/26, and 07/05. Measurements were always taken from 11.00 h to 13.00 h using the LI-6200 portable photosynthesis system model (LICOR Inc., USA).

Nitrogen determinations: The N concentration was determined on stems, leaf blades, petioles, and fruits collected every two weeks. Determinations were done using a modified Kjeldhal method (Bremer and Mulvaney, 1982).

Growth analysis: Every 14 days, four plants per treatment were measured destructively. Stems, removed leaves (separated into blades and petioles) and picked fruits were dried in a ventilated oven at 60 ºC for at least one week. The leaf area was measured with a Leaf Area Meter model LI- 3100 (LICOR Lincoln, NE, USA).

Fruit growth analysis: Starting at anthesis, three sets of flowers, separated by one week in age, were tagged. For each cohort, at least 60 flowers were tagged in each replicate (modified

from Heuvelink, 1995). Starting three days after anthesis and two times per week, two tagged fruits in each plot were randomly sampled at 8.00 h in the morning. Therefore, samples were collected at 3, 7, 11, 14, 18, 22, 26, 30, 33, 37, 41, 45, 49 and 53 DAA (days after anthesis). During sampling, the fruit diameter was measured, the fresh weight was recorded, and the dry weight was destructively determined.

Total yield: A total of 32 plants per treatment were selected for the final yield. At harvest, complete plants (8 per replicate) were harvested separately. The number of fruit was recorded for each replicate and classified according to fruit size. Fruit size designation was in agreement with the United States standards for grades of fresh tomatoes (Table 6-1). The fresh weight of fruits was recorded and 1 kg of fruit for each size designation was sampled for dry weight determination. The rest of each harvested plant was chopped and dry weight was determined in order to obtain the fruit harvest index at harvest.

Data analysis: Treatment comparisons were done using INFOSTAT statistical software and a Duncan means separation test at a significance of $p < 0.05$.

Results

Water Stress

Leaf water potential: Under water stress (WS) treatment, midday leaf water potential (Ψ_L) decreased to between -1.2 and -1.6 MPa. In well-watered plants undergoing control treatment (CT), it remained around -0.8 MPa (Figure 6-1). After re-watering, the Ψ_L in plants under WS increased. Approximately three days after re-watering, it reached similar although slightly lower values compared with plants under CT. In addition, the relative water content of leaves (RWC) from water stressed plants was 86%. This value was lower than the leaves from well-irrigated plants. The well-irrigated plants had an average RWC of 93%. The soil water content in WS conditions (Figures 6-2 and 6-3) was lower than the content of the soil under CT.

On average, CT soil maintained water content values between 0.10 and 0.14 cm^3/cm^3. The water content of the soil under WS reached values as low as 0.02 cm^3/cm^3. Even after re-watering, the content increased only to 0.08 cm^3/cm^3.

Gas exchange: The photosynthetic rate was 13% less in water stressed plants than well watered plants. Stomata resistance was 32% higher in water stressed plants than CT plants (Table 6-2 and Figures 6-4 and 6-5). Under water stress, the stomatal resistance was the most noticeable response of the leaves. The photosynthesis rate was less affected.

Total crop yield: In Table 6-3 and Figures 6-6, 6-7, 6-8 and 6-9, the results of the tomato plant growth and total fruit yield are presented for the different treatments. The total fresh fruit yield was significantly greater in CT than in WS. On average, water stressed plants produced 27% less (57.7 Mg ha^{-1}) than well watered plants (79.2 Mg ha^{-1}). The total dry fruit weight was also significantly different between WS and CT. However, the differences were less than those found in the fresh weight. The total above ground biomass and fruit dry weight was reduced by 22% and 24%, respectively. The maximum LAI was 15.5% lower in WS plants than in CT plants. The fruit number (measured as the fruit that reached commercial size) was reduced by about 20% in water stressed plants compared to CT plants. The harvest index was not significantly different between CT and WS treatments. This finding suggests that water stressed plants maintain relatively stable partitioning of dry matter to the fruits in spite of the stress.

The contribution of each class size to the total yield was different according treatments. Thus, during 2007 81 % of total fruit yield in CT corresponded to large, extra large and maximum large fruit classes comparing with 63% of contribution from these classes in WS treatment (Table 6-5).

Nitrogen Stress

Gas exchange: Photosynthetic rates were significantly reduced by N stress (Table 6-2; Figures 6- 4 and 6-5). The photosynthesis rate was reduced by 19.5% in N stressed plants compared with CT plants. The N stress increased the stomatal resistance by 23%. The photosynthesis reduction under N stress was less than reported by Scholberg *et al*. (2000). This report found a reduction of 30% in leaf photosynthesis in plants under severe N stress. A probable explanation is that even when the leaf N concentration in NS was significantly different from the CT, the N concentration was still above the critical level of 2%. Therefore, the leaf photosynthesis rate was expected (Taber, 2005). In addition, the residual fertility of the soil was not measured at the start of the experiment. Since the tomatoes were cultivated in the same field during previous year, the leaf N concentration might have been slightly higher than expected.

Total crop weight: In Table 6-3 and Figures 6-6, 6-7, 6-8 and 6-9, the tomato plant growth and total fruit yield are shown for the different treatments. Total fruit fresh yield was significantly less in NS than in CT. On average, N stressed plants produced 41% less fruit (45 Mg ha^{-1}) than N fertilized plants in CT (79.2 Mg ha^{-1}). Total fruit dry weight was also significantly different between NS and CT. The total biomass and the fruit dry weight were reduced by 46% and 59%, respectively by N stress. The average maximum LAI was 43% lower in the NS plants than the CT plants. This reduction in LAI had a lag of about four weeks in response to the N stress. In addition, the specific leaf area (SLA) was reduced by almost 50% in N stressed plants comparing with CT (Figure 6-7). The reduction in growth was not noticeable until about one month after the N stress was started (Figure 6-8). The fruit number was reduced by about 35% in N stressed plants compared to the CT. The harvest index was significantly different between the treatments. This finding suggests that nitrogen stressed plants reduced the partitioning of dry matter to the fruits under stress conditions.

The contribution of each class size to the total yield was different according treatments. Thus, during 2007 81 % of total fruit yield in CT corresponded to large, extra large and maximum large fruit classes comparing with 65% of contribution from these classes in NS treatment (Table 6-5).

Nitrogen concentration: The N treatment significantly changed the leaf blade N concentration. It did not change the N concentration in the petioles and stems. On average, the blade N concentration of N stressed plants was 20% lower than the N concentration in blades from well fertilized plants. Overall, the difference in the N concentration of the fruit in the varying treatments was less than in the blades and stems (Figures 6-10 to 6-13).

Growth of Individual Fruits under Water Stress

Fruit dry weight and fresh weight: There were observed differences in the means of the final fresh and final dry weights of the individual fruits. The data concerning with growth and development of fruits that began at different dates in the two treatment groups (WS and CT) are shown in Table 6-4. The fresh and dry weight per fruit differed significantly between treatments for the three cohorts. Fruits developed on WS plants achieved the lowest dry mass and fresh mass. The final dry mass of cohort number 1 in the WS treatment group was 17% lower than the same cohort of the CT plants (Figure 6-14). The final fresh weight of cohort number 1 from the WS fruits was 24% lower than the same cohort of CT (Figure 6-15). In cohort 2, the final DW achieved by WS fruits was 20% lower than the DW achieved by fruits under CT (Figure 6-16). The FW of cohort 2 in WS was 24% lower than the FW achieved by the same cohort under CT (Figure 6-17). Similar but more accentuated differences were observed in cohort 3 (Figures 6-18 and 6-19). For these late setting fruits, the mean final DW of the fruits from the WS was 24% lower than the fruits from the CT treatment. The fresh mass was 26% lower in the WS plants than the same cohort of CT.

Fruit dry matter concentration: The final fruit dry matter concentration was stable for the three cohorts across treatments (Figures 6-20, 6-21 and 6-22). On average, the DMC of the fruits from water stressed plants was higher than the fruits from CT conditions. Statistically, the differences were only significant for cohort 1 (not for cohort 2 and 3) (Table 6-4).

Fruit size: The final fruit size differed significantly between treatments for the three cohorts (Table 6-4). Quantitatively, fruit diameter was the variable that varied most between the treatments. Fruits developed from plants grown under WS achieved a smaller diameter (Figures 6-23, 6-24 and 6-25). On average, the final fruit diameter of fruits from WS plants was 27% lower than CT plants for cohorts 1 and 3. The same variable was 19% lower for cohort 2. These results agree with Ehret and Ho (1986), Mitchell *et al.* (1991) and Van Ieperen *et al.* (2005), who reported that water stress during growth of fruit reduced fruit size by 30%. Akaki *et al.* (2004) also demonstrated that water deficit resulted in smaller fruits with higher sugar concentrations.

Growth of Individual Fruits under Nitrogen Stress

Fruit dry weight and fresh weight: The observed differences in the means of the final fresh and final dry weights of individual fruits are presented in Table 6-4. Growth and development data of fruit that began at different dates for the two treatments (NS and CT) is presented in Table 6-4. The dry weight per fruit differed significantly between the two cohorts. Fruits developed from NS plants achieved the lowest dry mass and fresh mass. Statistically, only the differences in DW were significant. In contrast, the differences in FW were not. The final dry mass of cohort 1 in the NS treatment group was 23% lower than the same cohort in CT. The final fresh weight of cohort 1 in the NS group was only 5% lower than the same cohort in the CT group (Figures 6-14 and 6-15). In the case of cohort 2, the final DW achieved by fruits of NS was 26% lower than the DW achieved by fruits under CT. The FW of cohort 2 in NS was 7.5% lower than the FW achieved by the same cohort under CT (Figures 6-16 and 6-17). The latest

setting fruits remained small in plants under NS. No apparent growth was observed in those fruits. Apparently, the N stress affected the normal development of the latest fruits. Although no flower abortion was observed, no further growth after setting was observed.

Fruit dry matter concentration: The final fruit dry matter concentration was quite stable for the cohorts in both treatments (Figures 6-18 and 6-19). On average, the DMC of fruits from N stressed plants was lower than the DMC of fruits under CT conditions. Statistically, the differences were significant for both cohorts (Table 6-4). NS fruits showed a DMC 25% lower than CT fruits. The FW was not significantly different between treatments. This is related to the lower DMC of fruit from N stressed plants. The DW plants showed significant differences.

Fruit size: The final fruit size differed between treatments for the two cohorts. Fruits developed from the N stressed plants achieved lower diameter (Figures 6-23 and 6-24). On average, fruits in NS were 7.5% smaller than CT fruits for cohort 1. The fruits were 9% smaller for cohort 2. Although the difference was significant for cohort 1, it was not for cohort 2 (Table 6-4).

Discussion

Fruit growth: Water stress caused a significant decrease in fresh fruit weight and fruit size. Water stress also increased the dry matter concentration. Since the size of tomato fruits depends largely on water accumulation, it is not surprising that the size of the fruits was affected by water stress. Ehret and Ho (1986), Mitchell *et al*. (1991), Scholberg, (1996) and van Ieperen *et al.* (2005) reported similar results. Water stress had less effect on the dry matter accumulated by the fruits than the fresh weight. As a result of the reductions in size and fresh mass, the DMC of fruits increased in water stressed plants. Reduced fruit fresh weight as result of water stress is expected. Ho *et al.* (1987) explained that water stress produces an increase in fruit dry matter concentration because it increases the phloem sap concentration and decreases its flux. The

phloem flux is responsible for the increase in size of fruits via both water and carbon. More than 88% of fruit water acquisition is via phloem (Guichard *et al.,* 2001). Under water stress, the decrease in this flux produced smaller fruits that were higher in dry matter concentration. This finding was shown in our results. In addition, Guichard *et al.* (1999) showed that under water stress, the xylem flux to the fruits is reduced by 25%. The fruit transpiration is increased by 27%. As a result, the fruits reduce the net water accumulation via xylem by 30%. Akaki *et al.* (2004), published similar results. According to their results, in normally watered plants, the water accumulation of tomato fruits is 60% via phloem and 40% via xylem. Under water stress, the contribution of each pathway changes dramatically. In fact, 85% of the fruit water is acquired via phloem sap and only 15% via xylem. Under water stress, the water accumulated by tomato fruits is depressed by 36%. Why is the flux altered under water stress? For tomato fruit to grow there must be a total water potential gradient between the fruit and the rest of the plant (Grange and Andrews, 1994). Guichard *et al.* (1999) showed a close relationship between the fruit water potential and the daily flow of water toward the fruit. Johnson *et al.* (1992) also showed that the water potential gradient between the fruits and the plant controls the phloem-driven growth of the tomato fruits. The water potential of fruits is relatively unresponsive to the environment (Johnson *et al.*, 1992; Guichard *et al.*, 1999). Therefore, the flux depends largely on the stem water potential. Contrary to the fruit, the stem water potential is highly sensitive to water stress (Johnson *et al.*, 1992; Guichard *et al.*, 1999). In this study, we assumed that the reduction in the leaf xylem water potential in the WS was an indication that the stem water potential was lowered. It is possible that the driving force for water flow into the fruit may be reduced under WS. This may be the reason the FW and the size of individual fruits of water stressed plants were reduced. In our study, we observed that the fruits under WS ripened before the CT fruits.

The observed reduction in final dry weight may have been caused by a shorter growth period rather than a lower slope of growth rate. The results of Wolf and Rudich (1988) support this last assertion.

The effect of N stress on the growth of individual fruits was opposite to that of water stress. While the fresh weight and the volumetric size of fruits were slightly affected by N status, the dry weight and the DMC was significantly reduced in fruits of N stressed plants compared to N-supplied plants. However, the reduction in leaf photosynthesis rate was less than proportional to the reduction in dry weight. The LAI was largely impacted by N stress because leaf SLA was reduced. This change resulted in a decrease in LAI and no change in SLN. The reduced harvest index in N stressed plants may indicate that at least a portion of the reduction in dry weight may be explained by a lower partitioning of dry matter to fruits.

Crop total yield: This study showed that the impact of N stress on the growth and final yield of a tomato crops was greater that the impact of water stress. However, it is important to note that water stress was rather moderate and the N stress was severe. Therefore, no conclusions about the relative impacts of each stress should be made. The lower leaf area index, decreased biomass accumulation and yield reduction under N stress agrees with the results of Scholberg *et al*. (2000). This study showed that severe N stress significantly reduced LAI, biomass, and fruit yield of tomatoes grown in open fields.

The reduction in fruit yield may be due a double effect of N stress. The impact on the vegetative growth (leaf area) in turn reduced the accumulated biomass. The number of fruits that reached commercial size was reduced under NS compared with the control plants. The leaf photosynthesis rate of N stressed plants was moderately impacted. However the reduced SLA limited the LAI and canopy assimilation. This is likely the reason the number of fruits of

commercial size varied with the final yield. In addition, the harvest index was lower in N stressed plants than in well fertilized plants. This finding suggests that the partitioning of dry matter to the fruits was impacted by N stress. Studies by Huett and Dettmann (1988, 1989, 1991) and by Fujita *et al*. (2004) support that N stress affects the dry matter partitioning of vegetable crops, including the tomato. The FW and size of the fruits were relatively unaffected by N status. Therefore, these two variables affected the final yield less. In the case of WS, our study showed that it affected final yield through a reduction in the size and FW of the fruits. It had less effect on the number of fruits than the NS. In addition, plant growth and leaf photosynthesis rates were less affected than in N stressed plants. These two variables did not largely affect the final yield. In our experiments, the level of drought lowered the Ψ_L to -1.6 MPa. In other studies, it lowered it to -2.6 MPa or lower. This may be why the moderate and successively imposed drought during our experiment did not dramatically reduce the canopy growth and the leaf photosynthesis rate.

Summary and Conclusion

Our results are generally consistent with other authors concerning the effects of water and N stress on the growth of individual fruits, total plant growth and fruit yield. According to the results discussed above, a way to simulate water stress and N stress (indirectly) would be to reduce the stem water potential (to decrease the dry weight) and the phloem carbon concentration (to decrease the fresh weight). This approach seems feasible for hypothetical models that specifically simulate water and carbon fluxes into individual fruits. This is not the case for the CROPGRO -Tomato, which simulates the carbon balance at the whole plant level. This type of tomato model lacks phloem transport of carbon and water into the fruits. The fresh mass and fruit size are predicted from the single fruit DW. This prediction of DMC was described in Chapter 5. Consequently, in CROPGRO, it may be more feasible to simulate reductions in the single fruit growth indirectly. This could be achieved through reductions in the whole plant, the number of

fruits, the C partitioning or a combination of these factors. This model already uses reducing functions at the whole plant level. These functions include TURFAC/SWFAC (for water stress) and NSTRES (for N stress). While these functions have been well evaluated in relationship to plant growth and total yield, we need to explore how they may work in simulating the growth of individual fruits. In addition, empirical modifications of the relatively simple equations that simulate the DW, FW, DMC, and size of individual fruits need to be explored. These formulas may serve to mimic the dynamics of fruit growth under N and water stress.

Table 6-1. Standard size classes for fresh tomatoes in the U.S.

Size class	Diameter Minimum [a] ---mm---	Diameter Maximum [b] ---mm---	Diameter Minimum [a] ---in---	Diameter Maximum [b] ---in---
Extra small	48	54	1 28/32	2 4/32
Small	54	58	2 4/32	2 9/32
Medium	58	64	2 9/32	2 17/32
Large	64	73	2 17/32	2 28/32
Extra large	73	88	2 28/32	3 14/32
Max. large	88	-	3 15/32	-

Source: United States standards for fresh tomato fruit, in *Tomato Plant Culture*. Jones Jr. (1999).
[a] Will not pass through a round opening of the designated diameter when the tomato is placed with the greatest transverse diameter across the opening.
[b] Will pass through a round opening of the designated diameter in any position.

Table 6-2. Means comparison among three treatments for tomato leaf gas exchange and N leaf, stem and fruit concentration in Gainesville Fl, during spring of 2007.

Variable	Units	Control	Water Stress	Nitrogen Stress
Leaf photosynthesis	µmol m^2 sec^{-2}	29.9 a	26.0 b	23.8 b
Stomatal resistance	sec^{-1} cm	0.32 b	0.47 a	0.42 a
Leaf blade N conc.	%	3.13 a	3.02 a	2.51 b
Leaf petiole N conc.	%	1.73 a	1.67 a	1.48 a
Stem N conc.	%	1.85 a	1.78 a	1.67 a
Fruit N conc.	%	3.93 a	3.69 ab	3.28 b

Test: Duncan Alpha:=0.05 Different letters indicate significant difference between treatments (p<= 0.05)

Table 6-3. Means comparison among three treatments for tomato total above biomass, total fruit dry and fresh fruit yield, harvest index, fruit number and maximum LAI at harvest date on Jun 25 (NS), Jun 28 (WT) and Jul 05 (CT), in Gainesville, Fl, during spring of 2007.

Variable	Units	Control (CT)	Water Stress (WS)	Nitrogen Stress (NS)
Total above biomass	kg ha^{-1}	7137 a	5586 b	3810 c
Total fruit dry weight	kg ha^{-1}	4874 a	3694 b	1997 c
Total fruit fresh weight	kg ha^{-1}	79262 a	57715 b	46946 c
Maximum LAI	m^2 m^{-2}	3.57 a	3.02 a	2.04 b
Fruit number	units	57 a	46 b	37 c
Harvest index	kg kg^{-1}	0.69 a	0.67 a	0.52 b

Test: Duncan Alpha:=0.05 Different letters indicate significant difference between treatments (p<= 0.05)

Table 6-4. Means comparison among three treatments of growth variables of individual tomato fruit at harvest in Gainesville Fl, during spring of 2007.

Treatment	Cohort #1	Cohort #2	Cohort #3
		DW g fruit^{-1}	
Control (CT)	13.6 a	9.08 a	3.58 a
Water Stress (WS)	11.3 b	7.25 b	2.71 b
Nitrogen Stress (NS)	10.5 b	6.70 b	nd
		FW g fruit^{-1}	
Control (CT)	279 a	172 a	72 a
Water Stress (WS)	211 b	130 b	53 b
Nitrogen Stress (NS)	266 a	159 a	nd
		Fruit DMC (%)	
Control (CT)	4.8 b	5.0 a	4.6 a
Water Stress (WS)	5.3 a	5.5 a	5.1 b
Nitrogen Stress (NS)	4.0 c	4.2 b	nd
		Fruit Diameter (cm)	
Control (CT)	10.4 a	7.5 a	3.3 a
Water Stress (WS)	7.6 c	6.1 b	2.4 b
Nitrogen Stress (NS)	9.6 b	6.8 a b	nd

Test: Duncan Alpha:=0.05 Different letters indicate significant difference between treatments ($p <= 0.05$)

Table 6-5. Contribution of each commercial fruit size class to total yield fruit at harvest in Gainesville Fl, during spring of 2007.

Treatment	Fruit Size Class	Fresh Wt. kg ha^{-1}	Dry Wt. kg ha^{-1}	% of Total fresh yield	Number fruits as (%) of each class
Control					
	Cull	479	19	0.6	7
	Extra small	1494	55	1.89	8.8
	Small	3967	138	5	8.8
	Medium	9020	337	11.4	10.5
	Large	31980	596	40.5	26.3
	Extra large	15680	1892	19.9	29.87
	Maximum large	15993	678	20.3	9
Water Stress					
	Cull	573	30	1	17
	Extra small	1823	87	3.2	15.2
	Small	5018	234	8.7	8.7
	Medium	8070	371	14	19.4
	Large	17547	1330	30.5	21.7
	Extra large	15460	1200	26.8	17.4
	Maximum large	3393	548	5.9	2.4
Nitrogen Stress					
	Cull	917	38	1.96	16.2
	Extra small	1500	84	3.19	13.5
	Small	5025	175	10.7	8.1
	Medium	5823	207	12.4	10.8
	Large	14029	607	20.9	18.9
	Extra large	12707	539	27	19
	Maximum large	7962	255	16.9	10.8

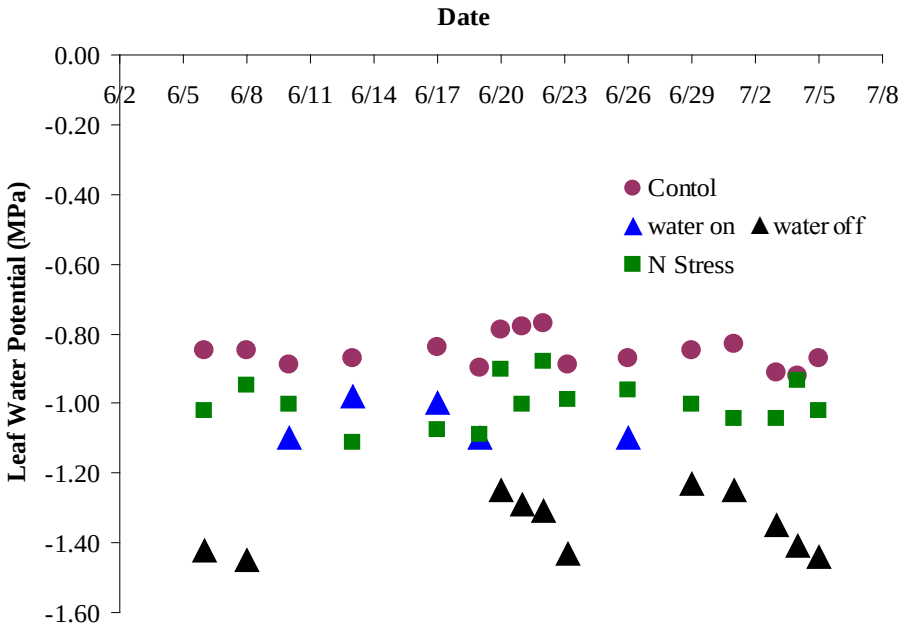

Figure 6-1. Leaf water potential of mature tomato leaves under three treatments in Gainesville Fl, during spring of 2007.

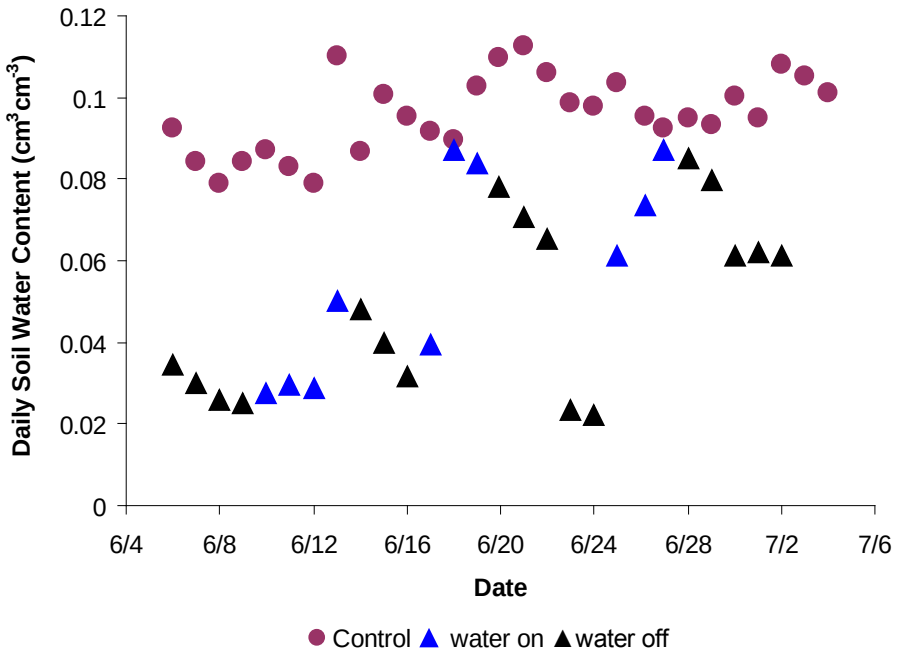

Figure 6-2. Daily soil water content based on 20 minute values from TDR probes buried at 20 cm depth, in experiments conducted in Gainesville Fl, during spring of 2007.

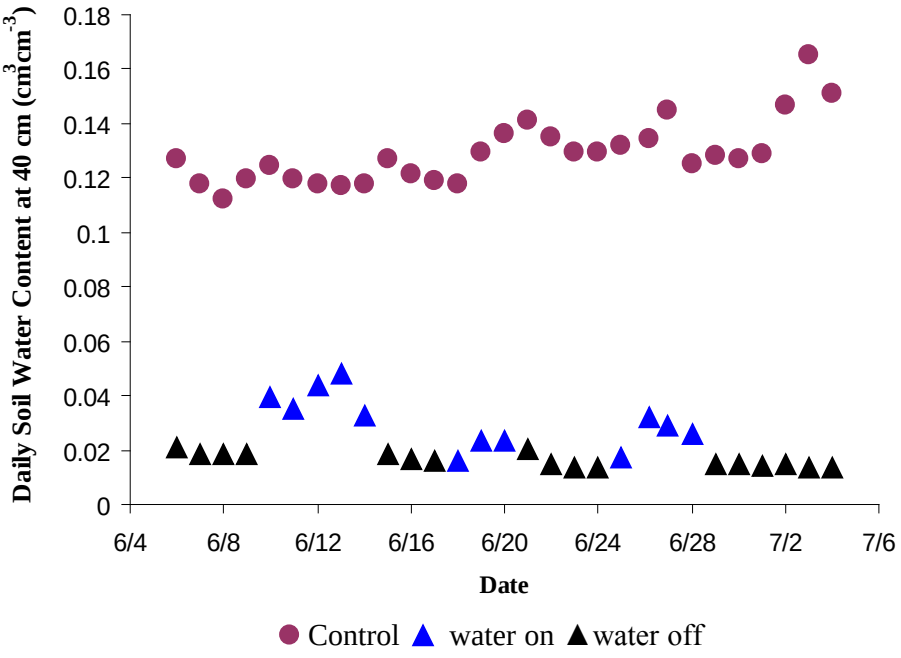

Figure 6-3. Daily soil water content based on 20 minute values from TDR probes buried at 40 cm depth, in experiments conducted in Gainesville Fl, during spring of 2007.

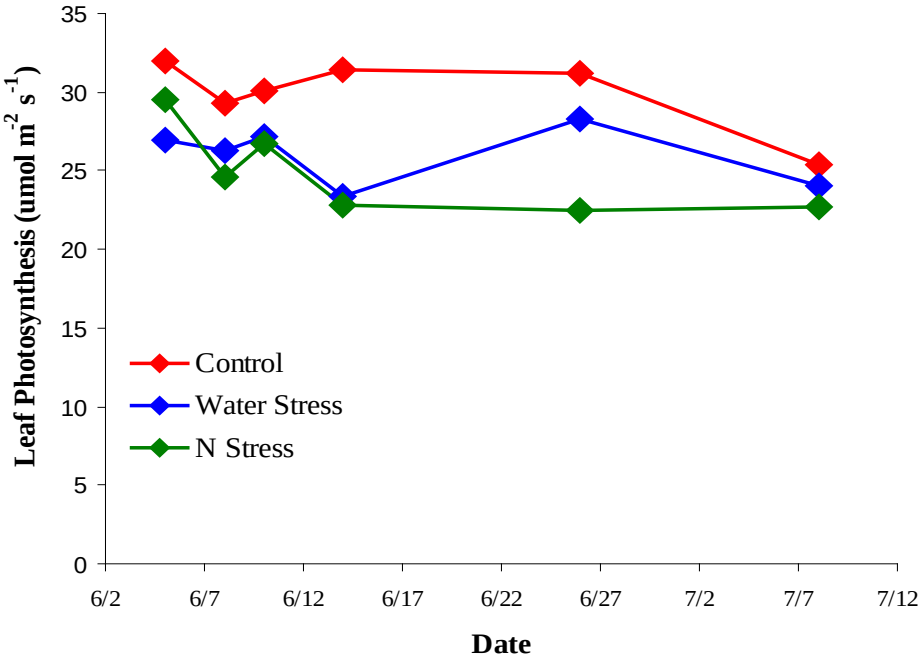

Figure 6-4. Photosynthesis rate of mature tomato leaves under three treatments in Gainesville Fl, during spring of 2007; symbols represent means of 16 leaves per treatment.

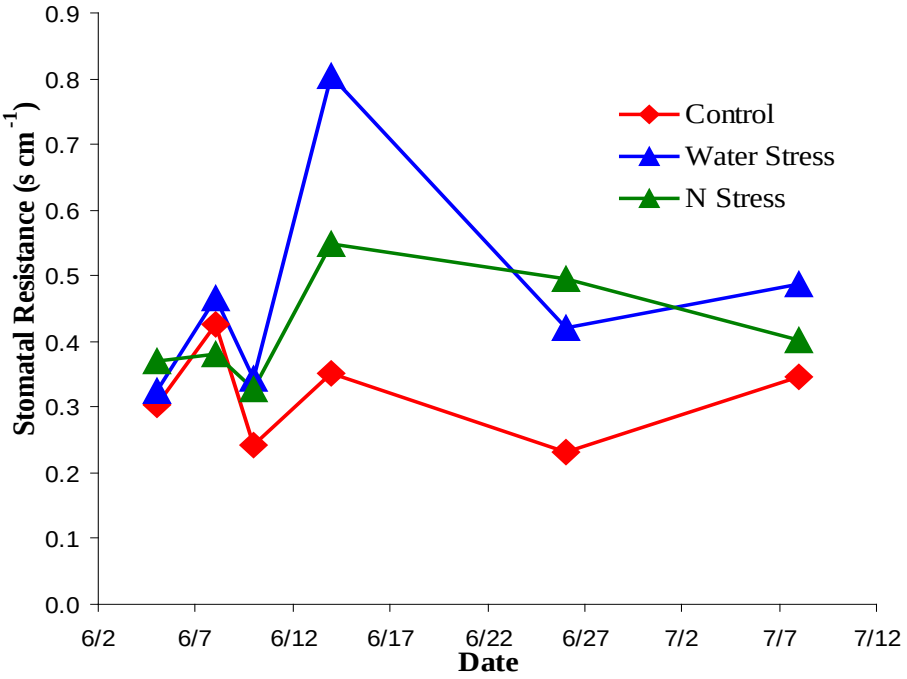

Figure 6-5. Stomatal resistance of mature tomato leaves under three treatments in Gainesville Fl, during spring of 2007 (symbols represent means of 16 leaves per treatment.

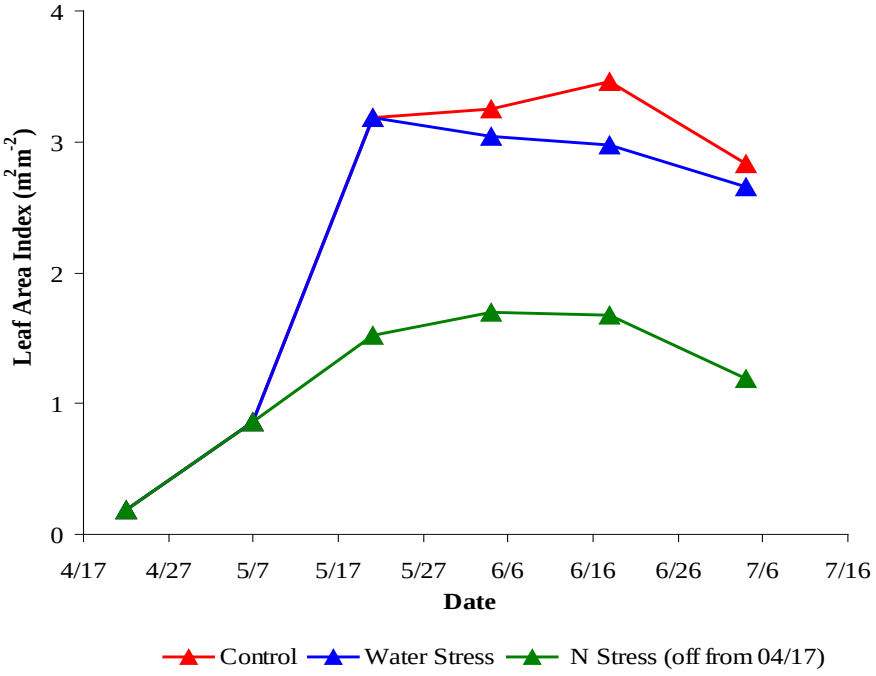

Figure 6-6. Effects of water and nitrogen on Leaf Area Index (LAI) over time of tomato plants in Gainesville Fl, during spring of 2007.

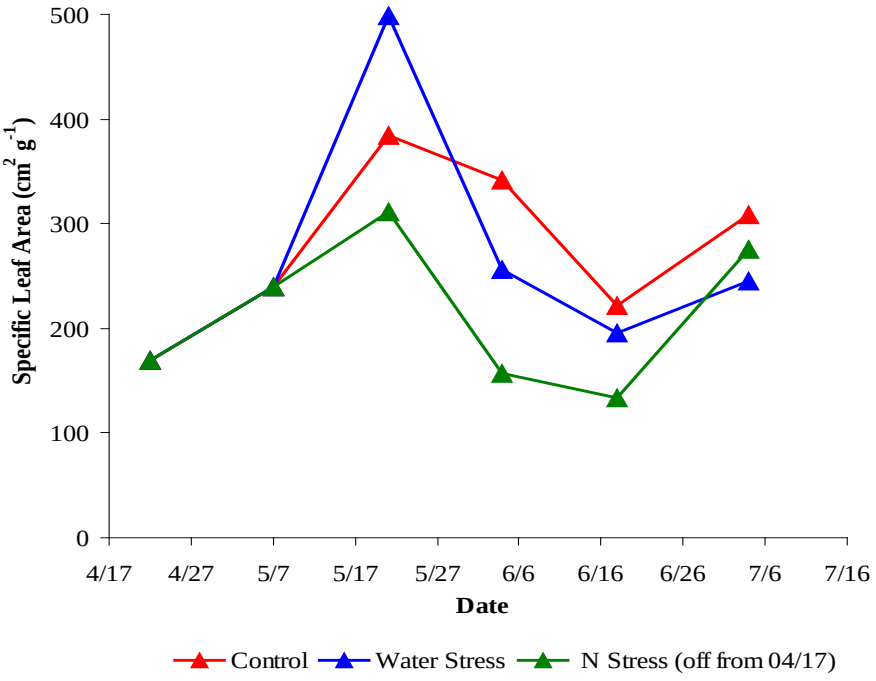

Figure 6-7. Effects of water and nitrogen stress on Specific Leaf Area (SLA) over time of tomato plants in Gainesville Fl, during spring of 2007.

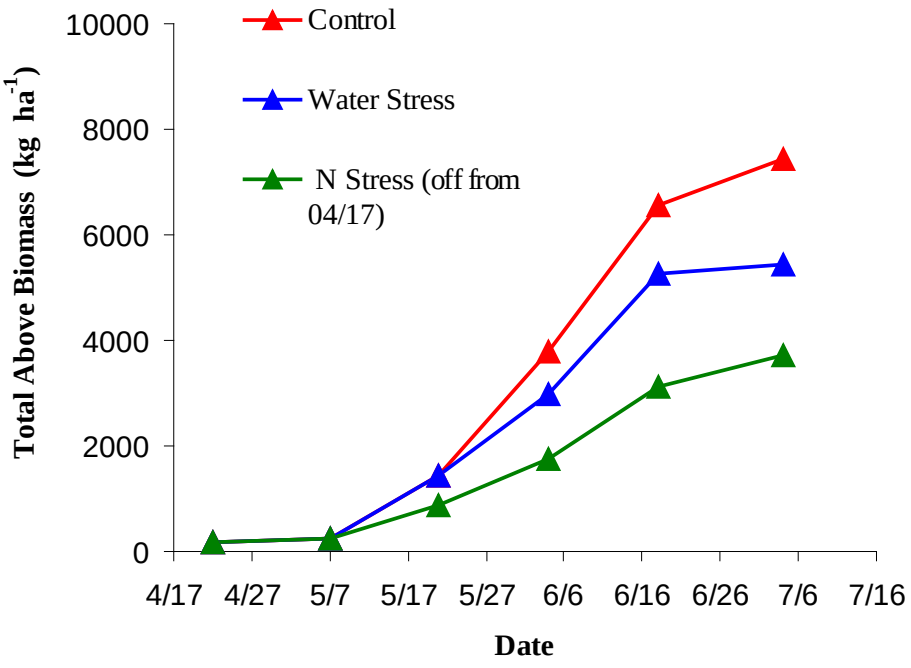

Figure 6-8. Effects of water and nitrogen stress on total above biomass over time of tomato plants in Gainesville, Fl, during spring of 2007.

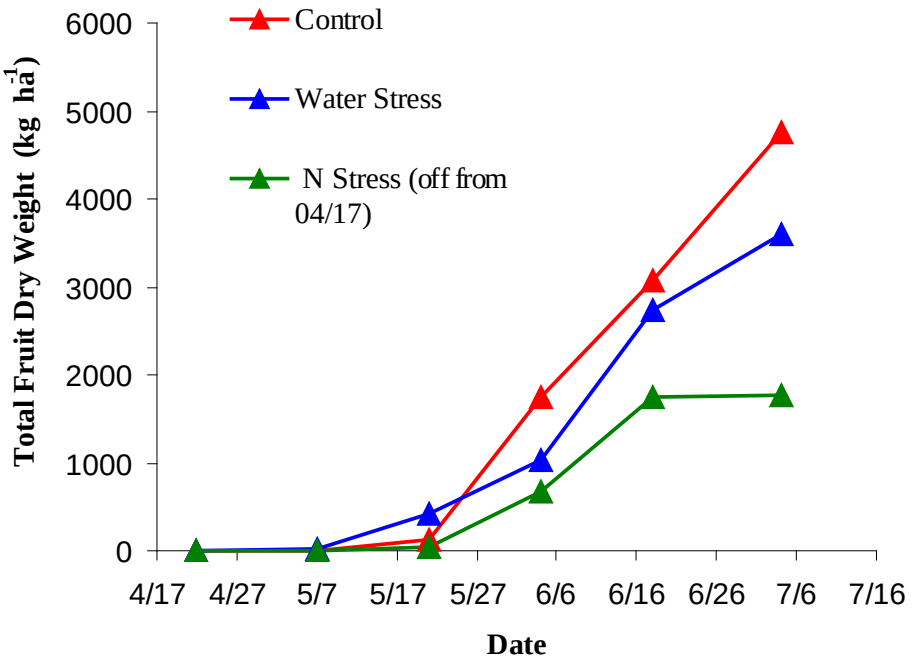

Figure 6-9. Effects of water and nitrogen stress on total fruit dry weight of tomato plants over time in Gainesville, Fl, during spring of 2007.

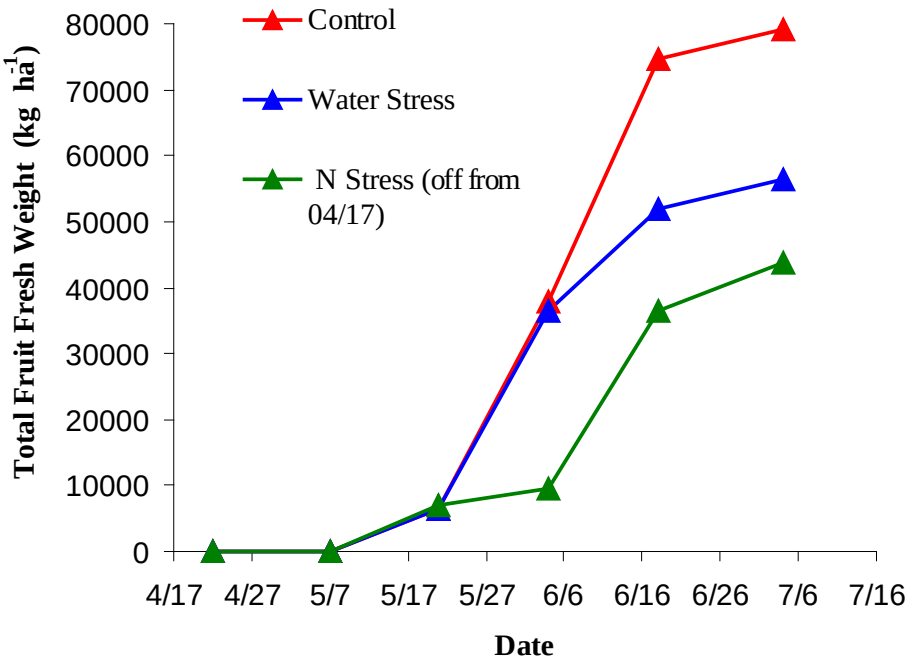

Figure 6-10. Effects of water and nitrogen stress on total fresh yield of tomato plants over time in Gainesville, Fl, during spring of 2007.

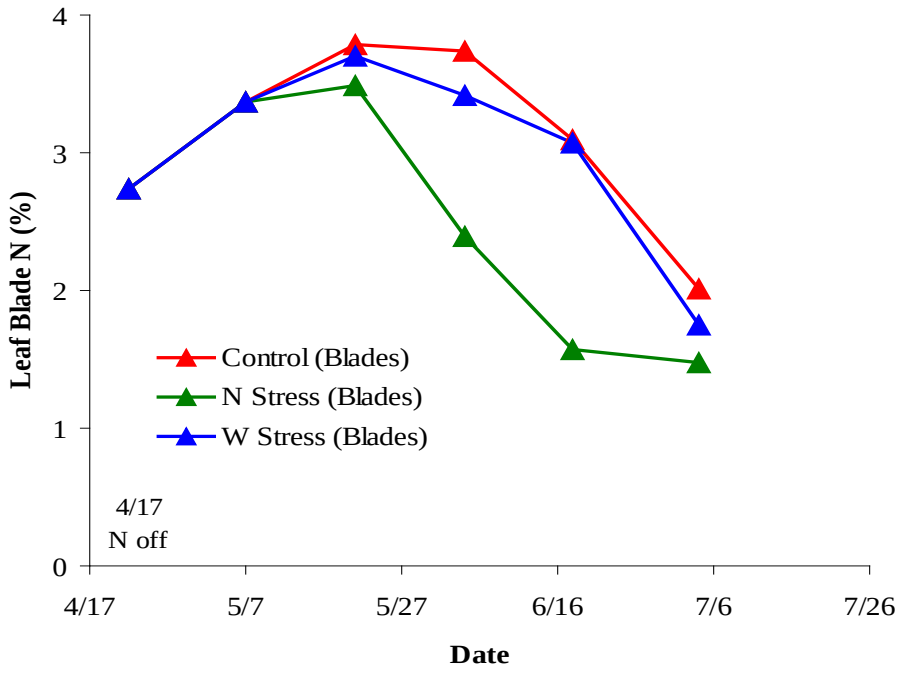

Figure 6-11. Leaf blades N concentration over time of tomato plants under N and water stress grown in Gainesville, Fl, during spring of 2007.

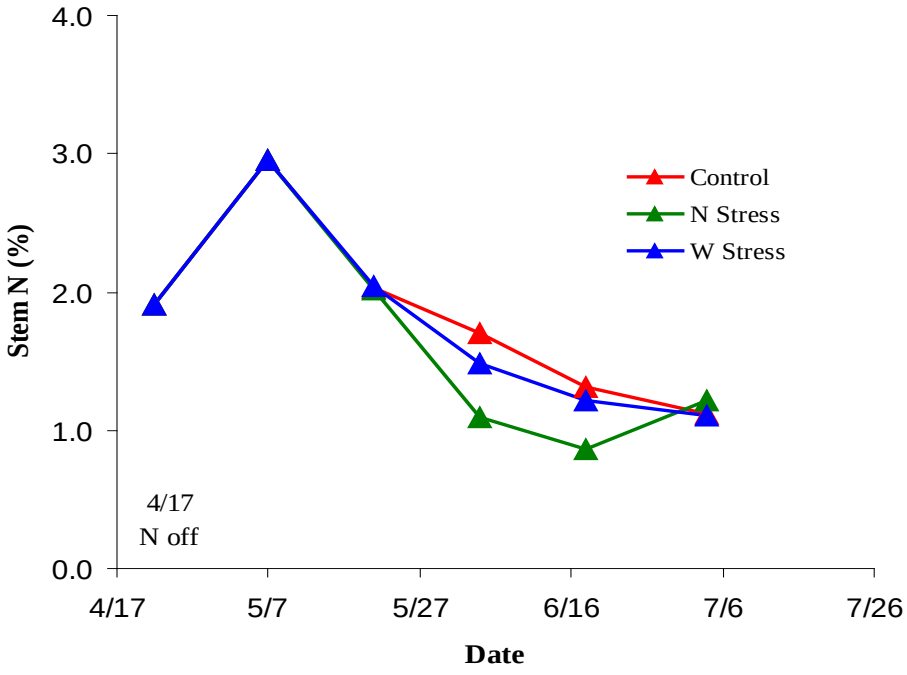

Figure 6-12. Stem N concentration over time of tomato plants under N and water stress grown in Gainesville, Fl, during spring of 2007.

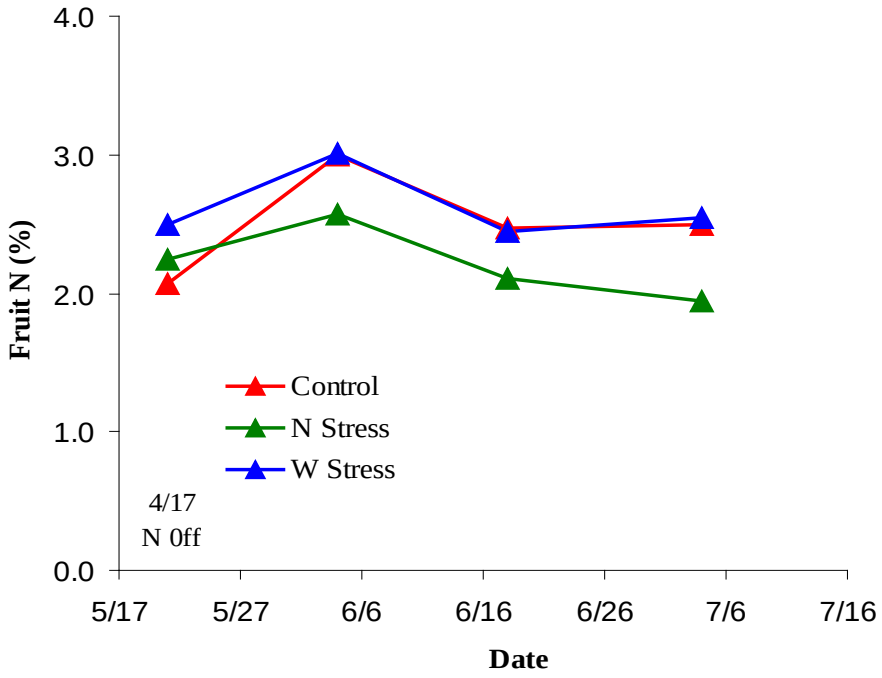

Figure 6-13. Fruit N concentration over time of tomato plants under N and water stress grown in Gainesville, Fl, during spring of 2007.

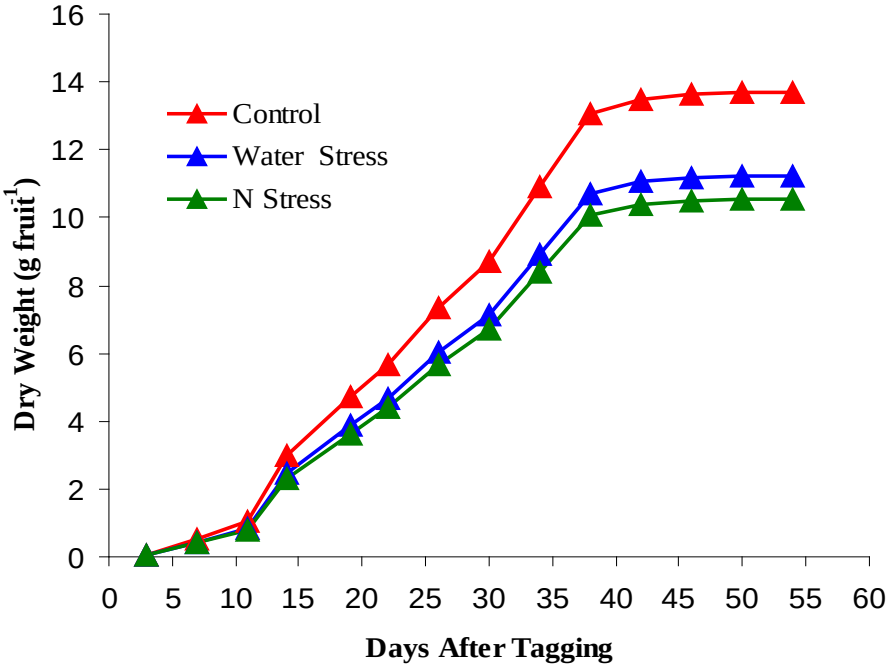

Figure 6-14. Effects of water and nitrogen stress on dry weight accumulation over time in individual tomato fruits for cohort number 1 in Gainesville, Fl, during spring of 2007.

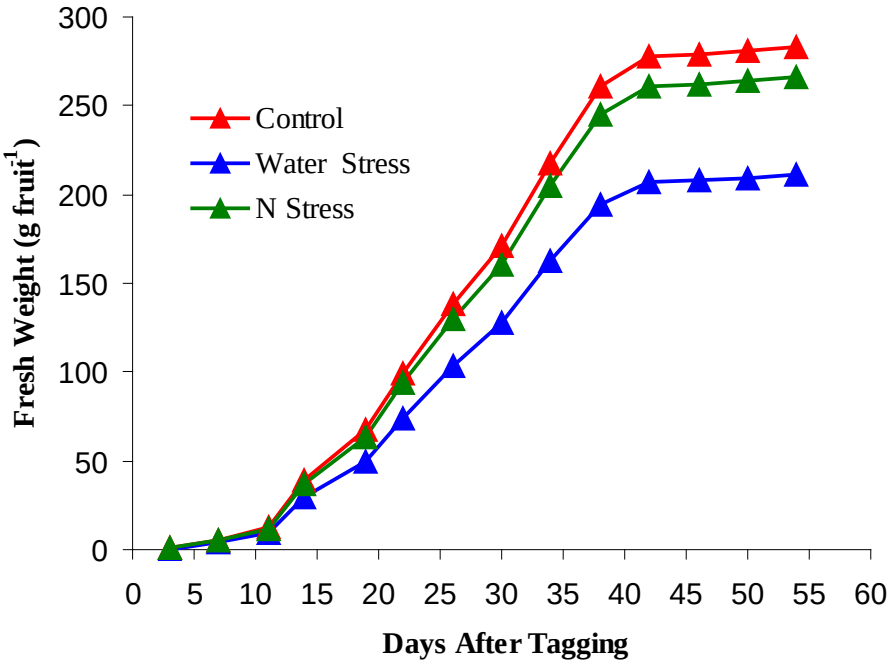

Figure 6-15. Effects of water and nitrogen stress on fresh weight accumulation over time in individual tomato fruits for cohort number 1 in Gainesville, Fl, during spring of 2007.

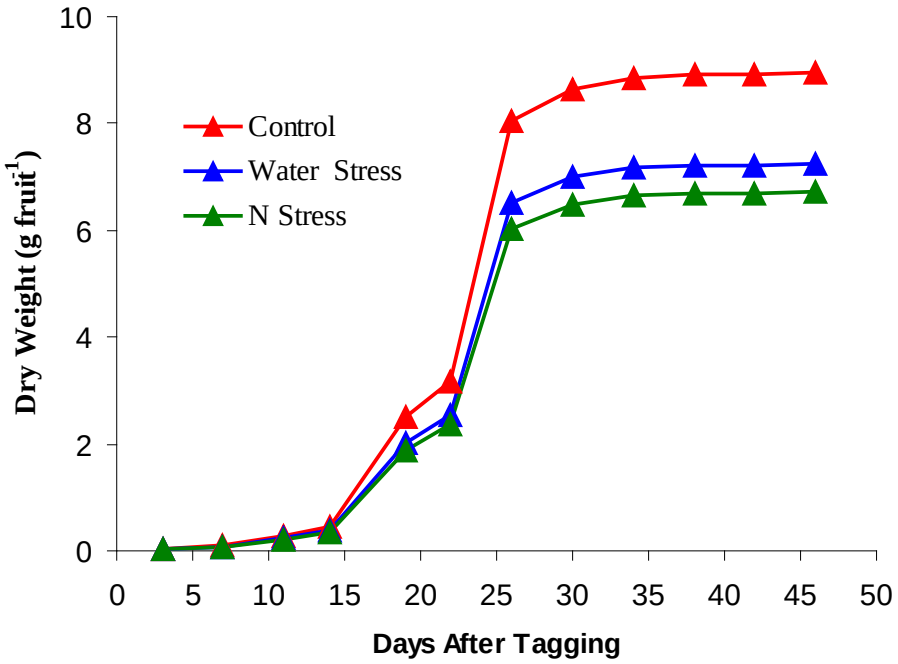

Figure 6-16. Effects of water and nitrogen stress on dry weight accumulation over time in individual tomato fruits for cohort number 2 in Gainesville, Fl, during spring of 2007.

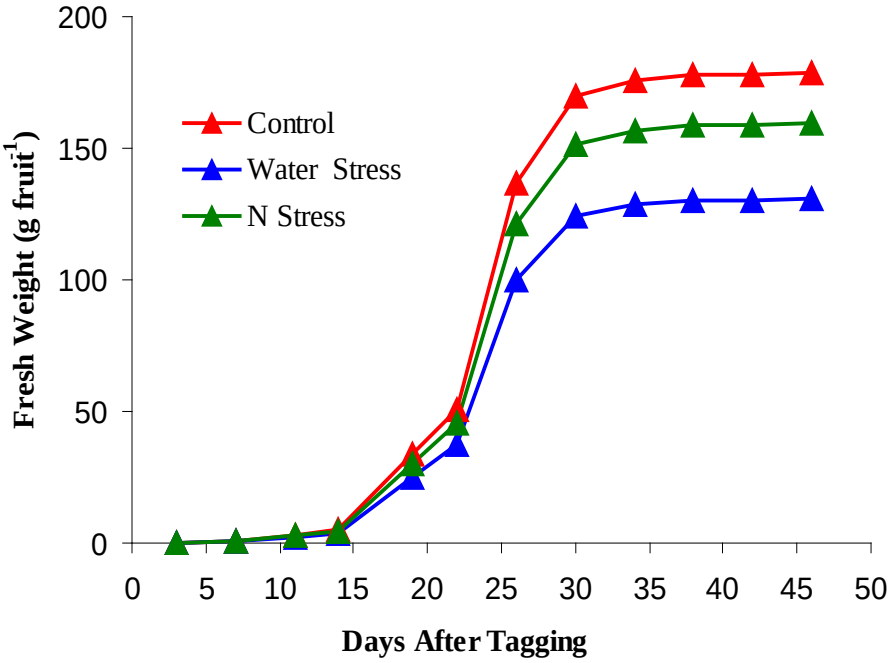

Figure 6-17. Effects of water and nitrogen stress on fresh weight accumulation over time in individual tomato fruits for cohort number 2 in Gainesville, Fl, during spring of 2007.

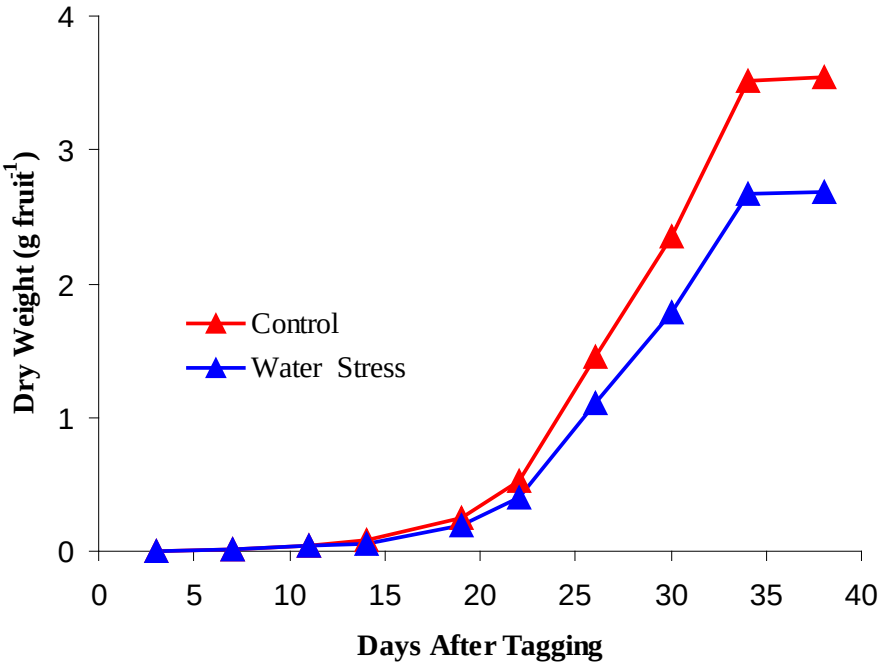

Figure 6-18. Effects of water stress on dry weight accumulation over time in individual tomato fruits for cohort number 3 in Gainesville, Fl, during spring of 2007.

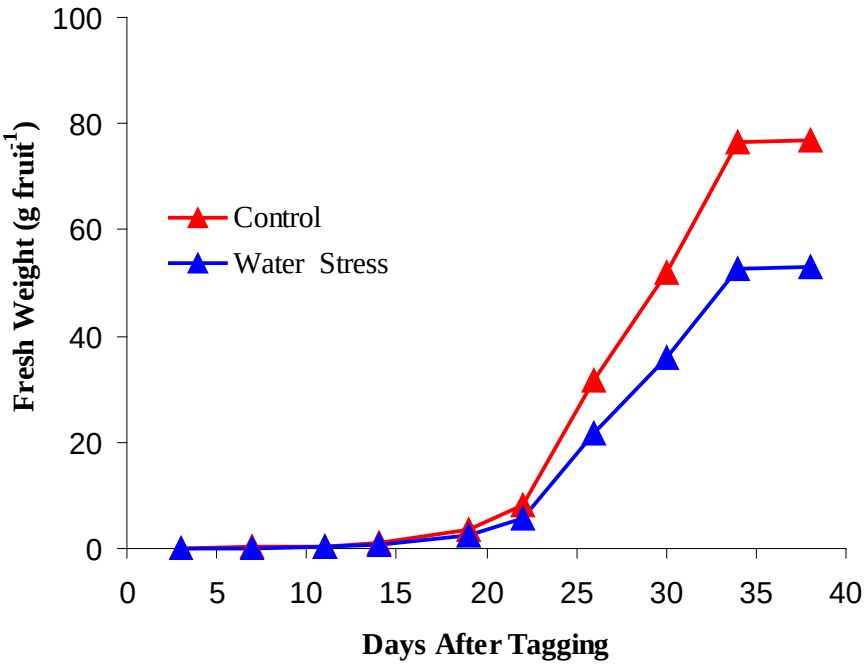

Figure 6-19. Effects of water stress on fresh weight accumulation over time in individual tomato fruits for cohort number 3 in Gainesville, Fl, during spring of 2007.

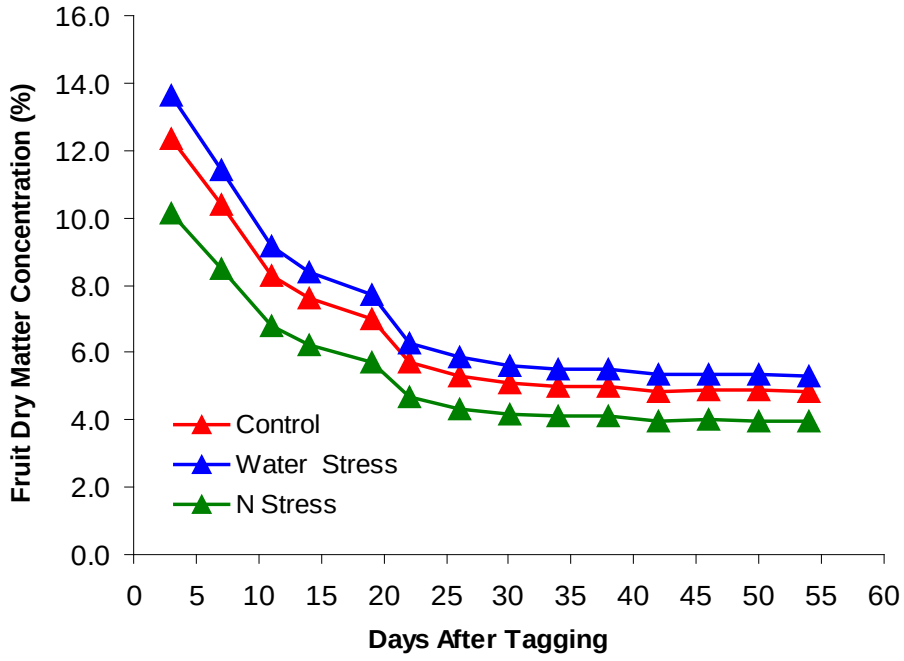

Figure 6-20. Effects of water and nitrogen stress on dry matter concentration over time in individual tomato fruits fro cohort number 1 in Gainesville, Fl, during spring of 2007.

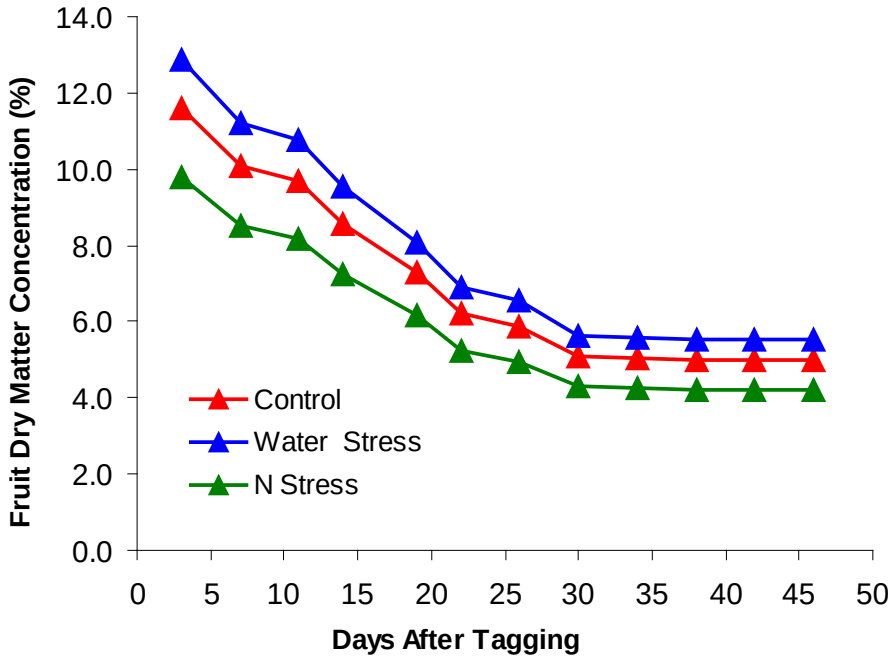

Figure 6-21. Effects of water and nitrogen stress on dry matter concentration over time in individual tomato fruits for cohort number 2 in Gainesville, Fl, during spring of 2007.

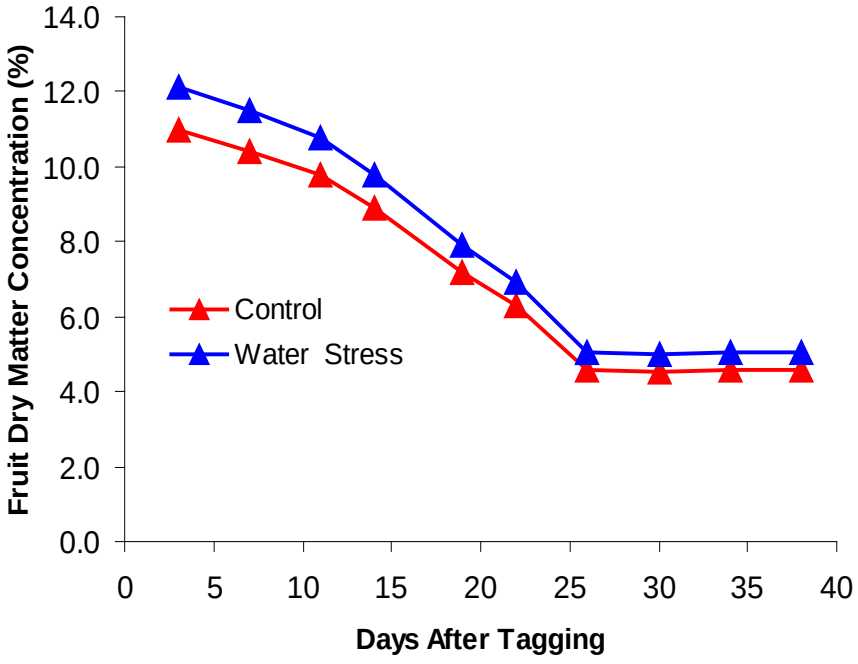

Figure 6-22. Effects of water stress on dry matter concentration over time in individual tomato fruits for cohort number 3 in Gainesville, Fl, during spring of 2007.

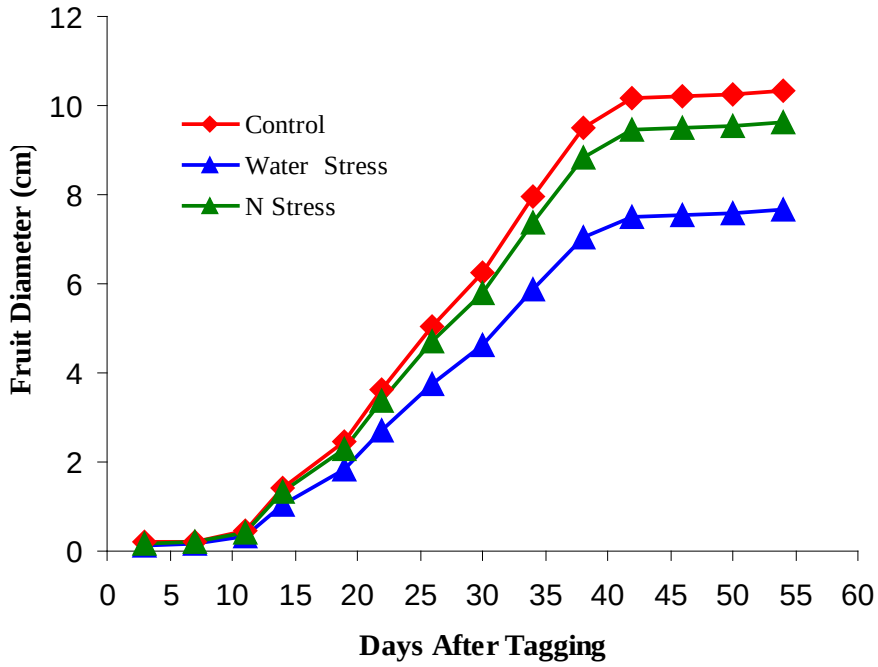

Figure 6-23. Effects of water and nitrogen stress on the diameter over time of individual tomato fruits for cohort number 1 in Gainesville, Fl, during spring of 2007.

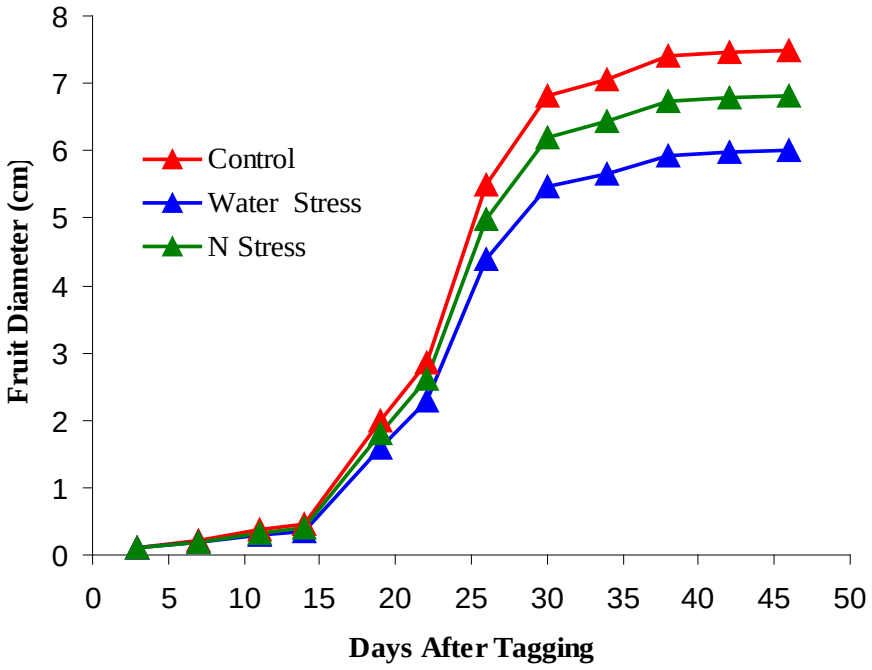

Figure 6-24. Effects of water and nitrogen stress on the diameter over time of individual tomato fruits for cohort number 2 in Gainesville, Fl, during spring of 2007.

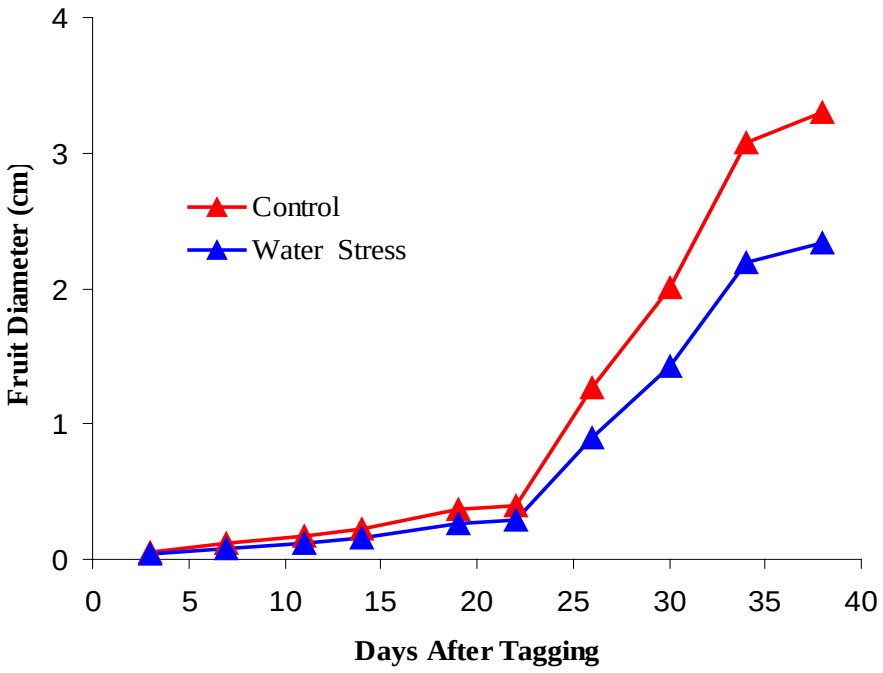

Figure 6-25. Effects of water stress on the diameter over time of individual tomato fruits for cohort number 3 in Gainesville, Fl, during spring of 2007.

CHAPTER 7
CROPGRO-TOMATO SIMULATION OF INDIVIDUAL FRUIT GROWTH UNDER WATER AND NITROGEN LIMITATIONS

Introduction

Size, water, and concentration of carbon compounds are the main criteria for assessing the quality of fresh fruits (Liu *et al*., 2007). For fresh market tomato, those variables also determine the production price, which largely depends on the size of the fruits. Tomato requires adequate water and nitrogen fertilization in order to obtain high yield and fruit quality. However, this goal is frequently not attained. In developed countries, because of the relatively inexpensive price of land inputs (a fact that may rapidly change according the economic crisis worldwide), leads the farmers to overuse both water and nitrogen resulting in leaching and often poor fruit quality because of fruit cracking and associated problems. In developing countries, on the contrary, because fertilizers and suitable irrigation systems are expensive, farmers tend to grow plants under varying levels of water and N limitation. In either situation, the result may be losses of fruit yield and quality. Suitable crop growth models may be valuable tools to understand the impact of water and N fertilization management on tomato production, and once validated, the results may be used to optimize resources and profits. However, quality traits are seldom subject to modeling, probably because they are the result of a poorly understood chain of processes (Struik *et al*., 2005). Rinaldi *et al*. (2007) have successfully utilized CROPGRO- tomato as decision support regarding N and irrigation strategies for processing tomato production in southern Italy. In a similar manner, CROPGRO has been used to study soybean and other legumes in the USA as well as in other countries. These applications have evaluated the ability of CROPGRO to simulate the response of plant growth to water and N stress in terms of total yield and biomass production. The growth of individual fruits in response to water and N

limitations, however, has been not studied although such a simulation may potentially contribute to optimize management of yield and quality of tomato fruits.

The results obtained in Chapter 6 indicated general responses of fruit growth to water and N stress compared with well-watered and fertilized plants. Based on those results, to adequately simulate the response to stress for individual fruit growth, a model must be able to: 1) create lag (slower fruit development) at the start of the growth period of the fruits under assimilate stress, especially for late-set fruits, 2) give priority for assimilates to older, first-formed fruits as compared with younger fruits on a cohort basis if stress is present, 3) reduce the fresh weight and size and increase the dry matter concentration of fruits under water stress and reduce the dry weight of fruits when plants are under N stress. In addition, the model should reduce the total fruit number and total fruit mass per plant under stress. In addition, the leaf expansion (leaf area index) as well as the specific leaf area should be also decreased under water and N stress. As result, a reduction of total biomass and total fruit dry weight is expected.

Currently, the CROPGRO model accounts for the effects of water deficit on the plant through several reducing factors proposed by Ritchie (1998) and called SWFAC (for effects on processes such as photosynthesis) and TURFAC (for effects of water deficit on expansive processes such as leaf expansion). Every day, the model computes the ratio between the root water uptake (supply) and the evapotranspirative demand. The ratio needs to be at least 1.0 in order to maintain photosynthesis (dry matter accumulation) at a normal rate, and 1.5 for expansive growth to be at its potential. A similar approach is used in CROPGRO to compute daily N stress. In this case, the reducing factor is called NSTRES, the model internally computes the daily ratio between the N uptake by the roots (and N-fixation if a legume) and the N demand for dry matter growth. When the ratio between N uptake and N demand falls below a certain

threshold to ensure a target N concentration in tissues grown today, an NSTRES value less than 1.0 results, and tissue N concentration is reduced and the growth is decreased. At a first look, this factor combined with reduced partitioning to fruits, may be useful to indirectly mimic the reduction in dry weight that fruits experienced under N stress. Indirectly the fruit number also may be affected because effects on fruit abortion may occur when the carrying capacity of the plants is limited due to a low N supply and also low assimilation rate. The impact on water accumulation of fruits under water stress, however, may be more difficult to simulate because there is currently no connection between CROPGRO's simulation of water stress and actual water accumulation in individual fruits. Water accumulation in fruits is not directly simulated by the model but rather inferred from the dry weight and the computed dry matter concentration. It may be feasible to use the SWFAC or TURFAC as factors/signals to affect dry matter concentration, and as a result alter the fresh mass and size. For these signals to work adequately, they need to affect also the timing of reproductive events under stress. Thus, it may be necessary to increase the lag at the start of the growth period for later-set fruits, but then to accelerate the maturation process resulting in a similar or even shorter total fruit growth period. It may be possible to modify the equations for dry matter concentration, fresh mass and fruit size (presented in the Chapter 5), using these water and N stress factors to mimic stress effects. This approach will be followed in this chapter, however, additional experiments may be needed in order to define the proportionality factors to improve accuracy because there are many possible scenarios of stresses. The objective of the present Chapter is to analyze the capability of the CROPGRO-Tomato model to simulate the growth of individual fruits when plants face water or N stress, and if needed to study possible mechanisms for overcoming the limitations of the model.

Materials and Methods

Experimental data: The data used for model evaluation were derived from field experiments carried out at the University of Florida Plant Science Research and Education Unit in Citra, Florida (29◦ 25' N, 82◦ 10' W) during the spring of 2007. The three treatments, control (CT), water stress (WS) and nitrogen stress (NS), as well as the experimental conditions and the measurements were fully described in Chapter 6. In addition, in Table 7-1 the characteristics of the soil series Tavares which correspond to the experimental site are presented.

The model: The version of CROPGRO-Tomato model as described in Chapter 5 was used in this study. No new calibration of genetic coefficients was needed because the same cultivar, season, location and experimental conditions as described in Chapters 5 and 6 were evaluated. In order to study the response of the model to water and N stress, the model was first run without any modification of parameters using the observed weather, irrigation, N application, soil water holding and N supplying traits of each experimental treatment. The outputs of the model were compared with observed data for a preliminary assessment of the model.

Model modification: Following the above comparison, several strategies were tested to improve the ability of the model to reproduce the effects of water deficit and N limitation on dry weight growth, fresh mass growth, and size of individual fruits. The following modifications were made to the model:

1) In the DEMAND routine of CROPGRO, which calculates the carbon and N demand for vegetative and reproductive growth, the maximum shell (fruit without seed) growth rate was allowed to be reduced by SWFAC and NSTRES modifiers to reduce the potential growth rate under water or N deficit according to the following equations:

$$GRRAT1 = SHVAR * TMPFAC \quad (7\text{-}1)$$

$$GRRAT1 = SHVAR * TMPFAC * (1 - (1 - (SWFAC) * 0.4)) * (1 - (1 - (NSTRES) * 0.2)) \quad (7\text{-}2)$$[1]

Where Equation 7-1 is the default equation in CROPGRO and Equation 7-2 is the one modified by stress signals. For the default model, this potential fruit growth rate (GRRAT1) is only dependent on temperature, although subsequently, actual fruit growth rate can be limited if C or N supply is insufficient to grow that cohort today. According to equation 7-2 when plants face water stress or N stress the maximum growth rate of fruits will be reduced proportionally to the values of SWFAC or NSTRES. The modifiers 0.4 and 0.2 are empirical and were solved through sensitivity analysis comparing outputs of the model with real data.

2) The physiological age of the fruits is related to stress by computing thermal time accumulators that are differently affected by water or N stress, and calling them if needed. In the default model, only one thermal time accumulator (PHTIM) is used (Eq. 7-3). By allowing different thermal time accumulators to operate, it is possible to affect the physiological age of the fruits in such a way that the developmental age may be accelerated or slowed as a function of SWFAC or NSTRES (Eq. 7-4). This last modification was connected to the function for computing the dry matter concentration of individual fruits as a function of physiological age (PAGE) in the FRESH WEIGHT subroutine of the model (see Chapter 5). The physiological age of the fruits is the independent variable of the equation and can potentially be different depending on water or N stress.

---

[1] GRRAT1 is the maximum growth per individual shell (g/shell/day)

SHVAR is the genetic potential shell growth rate during its rapid growth phase, with all conditions optimal, (g/shell/day)

TMPFAC is a modifier of genetic maximum growth rate for shell depending on temperature

NSTRES is the N stress factor, computed in the CROPGRO subroutine using total vegetative and reproductive N demand, (1.00=no stress, 0.0=max stress)

SWFAC is the effect of soil-water stress on photosynthesis, (1.0=no stress, 0.0=max stress)

$$PHTIM(DAS-NR2+1)=PHTIM(DAS-NR2)+TDUMX \quad (7\text{-}3)$$

$$PHTIM1(DAS-NR2+1)=PHTIM1(DAS-NR2)+TDUMX * (1-(1-(SWFAC)*0.3))*(1-(1-(CNSTRES)*0.1)) \quad (7\text{-}4)$$[2]

Where Equation 7-3 is the default equation in CROPGRO and Equation 7-4 is the one modified by stress signals. The modifiers 0.3 and 0.1 are empirical and were solved through sensitivity analysis comparing outputs of the model with real data.

3) Finally, the dry matter concentration was allowed to respond to the SWFAC and NSTRES factors by including SWFAC and NSTRES in the equation for computing dry matter concentration in such a way that the dry matter concentration is increased under water stress and reduced under N stress in agreement with measured data (Eq. 7-5 and 7-6).

$$DMC=5+10*EXP\left(-7.1*\frac{PAGE-1.6}{55}\right) \quad (7\text{-}5)$$

$$DMC=5+1.5*\left(1-\frac{PAGE1}{PAGE}\right)-1.5*(1-NSTRES)+10*EXP\left(-7.1*\frac{PAGE1-1.6}{55}\right) \quad (7\text{-}6)$$

[2] PHTIM is cumulative photothermal time in ages of seeds and shells, the default accumulator

PHTIM1 is cumulative photothermal time in ages of seeds and shells modified by water and N stress (updated accumulator)

DAS are the days after start of simulation, NR2 is days when 50 % of plants have one fruit

(fruit) (d)

TDUMX is the photo-thermal time that occurs in a real day based on early reproductive development temperature function

CNSTRES is the N stress factor computed as an 8 days moving average

Where Equation 7-5 is the default equation in CROPGRO and Equation 7-6 is that modified by the stress signals. The PAGE and PAGE1 are the photothermal ages of each cohort and are defined by

PAGE= PHTIM(NR2TIM+1)-(PHTIM(NPP) (7-7)

PAGE1= PHTIM1(NR2TIM+1)-(PHTIM1(NPP) (7-8)

**NPP is the cohort number used as an index in loops

The value 1.5 in equation 7-6 is an estimated value based in our observations of real data for increases in DMC of fruits under water stress, where the ratio PAGE1/PAGE carries the cumulative water stress (SWFAC) from Equation 7-4 into Equation 7-6 and the -1.5 value causes decreases under N stress.

To test these strategies, comparisons of simulated and observed growth of individual fruits as well as growth of the whole plant and total fruit yield were evaluated using RMSE and Willmott index as criteria of evaluation.

Results and Discussion

The results of the control treatment were discussed in Chapter 5 and are not discussed again in this section. However, they are presented in the figures for comparative reference with stress treatments and to verify that the model modifications based on SWFAC and NSTRES factors did not affect simulated shell growth, fruit age and dry matter concentration of the control treatment, but did affect simulated variables as intended to mimic the observed data of the water and N stress treatments.

Water Stress

Whole plant level: The CROPGRO Tomato model was able to reproduce the reduction in growth observed in tomato plants under water stress as compared with well-irrigated plants. As shown in Figure 7-1, the model was able to reproduce accurately the effect of water stress on leaf

expansion and LAI compared to measured data over time. In addition, the variation of LAI over time was well simulated by the model as revealed by the high d index and the low RMSE of the predictions. Similarly, the total above biomass (Figure 7-2) and total fruit dry weight (Figure 7-3) during the season were very well predicted by the model with a d index close to the optimal value 1 and low RMSE for both variables. Figure 7-4 shows the results for predicted total fruit fresh weight, showing that simulated total production of fruit fresh weight corresponded well to that measured on plants under the water stress treatment. The total fruit fresh weight is a result of (summed over) the number and fresh weight of individual fruits. Therefore it is possible that this response is not only to the water deficit at the whole plant level but also to the newly added modifiers for affecting the growth of individual fruits and dry matter concentration.

Individual fruit dry weight: Observed and simulated dry weight accumulation in individual fruits from flowers that had been tagged at three weekly dates in plants under water stress treatment are presented in Figures 7-5, 7-6, and 7-7. There was a good correspondence between simulated and observed data for cohort numbers 1 and 2. In these cohorts, the Willmott agreement index (d) was close to an optimal value 1. The high d value indicates that the variability in the observations around the mean was well tracked by the predictions and therefore the model was able to reproduce the timing of when the fruit growth was affected by water stress. The average RMSE for cohorts 1 and 2 was low and represents a model error of 9.5 % of the final fruit dry weight for these cohorts. A less satisfactory response of the model was for cohort number 3, which gave an unacceptable d value (less than 0.9) and a RMSE that represents an error of 26 % of the final DW for this cohort. The poor simulation for this cohort has only minor implications for predictions of total fruit yield because the contribution of the late-set fruits to the total yield is small and represented less than 4 % of the total yield in the control

treatment during 2007 and even less in the water stress treatment (data not shown). The results show that the model is able to give priority to earlier cohorts over later-formed cohorts when carbon supply is compromised by water deficit. This is noticeable because cohort number 3 started to grow very late in the cycle after the earlier cohorts reached their constant final masses. The results for simulation of dry weight gain of individual fruits under water stress is basically a result of reduction of C availability at a whole plant level combined with minor effects on the maximum shell growth rate in the DEMAND routine, for which the later rate was reduced as a function of SWFAC.

Fruit dry matter concentration: Observed and simulated dry matter concentration in individual fruits from flowers that had been tagged at three weekly dates in plants grown under water stress are presented in Figures 7- 8, 7-9 and 7-10. The model was able to mimic the increase in dry matter concentration observed in fruits under water stress, as was shown in the experimental results. Simulated and measured data agreed reasonably well with a RMSE of 0.6 % for cohorts 1 and 2, respectively, which represents a model error of 12 % of the final fruit DMC for these cohorts. The higher error RMSE (1.0 %) was for cohort number 3 and this error represents 20 % of the final fruit DMC for these fruits. The Willmott index was high for all cohorts. The main factor improving the prediction of dry matter concentration was the addition of a SWFAC- dependent modifier to the equation 7-6 for computing the dry matter concentration of individual fruits. The SWFAC modifier used cumulative SWFAC over the fruit growth cycle to affect dry matter concentration over time, which gave an improved prediction and higher dry matter concentration under water stress. An alternative function using the current daily value of SWFAC did not work well, as it gave intermittent or bumpy instantaneous increases of DMC following daily variations in SWFAC (equation not shown). These simulations confirm the

concept of cumulative water deficit (memory) effects on DMC increase over time. The memory effect was created by carrying different thermal time accumulators into the FreshWt subroutine, one with the stress signal incorporated with the thermal accumulator, and one without the stress signal (the default PHTIM), and dividing the first by the latter (Eq. 7-6). This approach worked well to reproduce cumulative effects of stress rather than instantaneous effects.

Fruit fresh weight: Observed and simulated fresh weight accumulation in individual fruits from flowers that had been tagged at three weekly dates in plants under water stress are presented in Figures 7-11, 7-12, and 7-13. Measured data show that fresh mass and fruit size of individual fruits were the variables most affected by water stress. There was a very good correspondence between simulated and observed data for cohorts 1 and 2. In these cohorts, the Willmott agreement index (d) was equal to 0.97. The average RMSE for both cohorts was low (12 g) which represents an error of 7.4 % of the single fruit final fresh weight. Similar to dry weight prediction, less satisfactory results occurred for cohort number 3.

The good performance of the model in reducing the fresh weight of individual fruits under water stress was related to a combination of steps 1 to 3 described in Material and Methods section. First and most important is related to the increased dry matter concentration, created by linkage to the cumulative SWFAC signal (Eq 7-6). However, that was not enough to produce the desired magnitude in reduction of fresh mass growth over time, as dry matter growth was also slightly reduced which was linked to reduction in the maximum fruit (shell) dry matter growth rate (GRRAT1) under water stress (Eq 7-2).

Fruit size: Observed and simulated individual fruit diameter from flowers that had been tagged at three weekly dates in water stressed treatments are presented in Figures 7-14, 7-15 and 7-16. Comparisons among cohorts showed that the fruit sizes of cohorts 1 and 2 were well

simulated by the model although the fruit diameter was slightly underestimated. The average RMSE was 0.92 cm for both cohorts, which represents a model error of 14% for the fruit diameter for both cohorts. The average d value was 0.97 indicating that the variability in the experiment was well captured by the predictions. The fruit size simulation of the cohort number 3 was poor as result of the poor simulation of fresh weight for this cohort.

Nitrogen Stress

Whole plant level: The N stress factors in CROPGRO were suitable to reproduce the reduction in total biomass and total fruit growth observed in tomato plants under N stress as compared with well N fertilized plants. As shown in Figure 7-17, the model was able to reproduce the effect of N deficit on leaf expansion and simulated LAI over time, although LAI was slightly overestimated for the control. In addition, the variation of LAI over time was well simulated by the model as revealed by the high d index and the low RMSE of the predictions. The total above biomass (Figure 7-18) was over-estimated by the model, in part, because under N stress the model accumulates large amounts of carbohydrate in stems when insufficient N is available for new tissue growth. On the other hand, the model gives fruits first priority for N and assimilate, and the total fruit dry weight (Figure 7-19) during the season was very well predicted by the model with a d index close to the optimal value and a low RMSE. Figure 7-20 shows the results for predicted total fresh weight. The total production of fruit fresh weight was reasonably well predicted under the N stress treatment. Fruit fresh weight in the model is calculated from the dry weight growth and the dry matter concentration for individual fruits and then total fruit fresh weight in the model comes from summing fresh weights over all fruit cohorts/numbers present. A good response of the model was the simulated reduction in carrying capacity of the crop as the simulated number of fruits under N stress was 62 % less than in control plants, which reduction was close to experimental results (data not shown). The reduction in total fruit fresh weight in

plants under N stress is a direct consequence of 1) the reduction of canopy expansion and photosynthesis under N deficiency, which affected the carbon availability and the N supply itself for adding the next fruit. In addition, NSTRES was used as a factor to reduce the potential growth rate of individual fruit in the DEMAND routine. The N deficit did not appear to affect fruit physiological age or timing. Therefore, the reduced growth under N stress is less related to a different growth timing of fruits as compared with fruits under water stress conditions.

Fruit dry weight: Observed and simulated dry weight accumulation in individual fruits from flowers that had been tagged at three weekly dates in plants grown under N stress treatment is presented in Figures 7-21 and 7-22. There was a good correspondence between simulated and observed data for cohort number 1. For this cohort the Willmott agreement index (d) was 0.98. The RMSE was low and represents a model error of 9 % of the final fruit dry weight for cohort 1. The response of the model for cohort number 2 was poor, the model was able to reproduce stress, but the N stress response was too strong in the mid-cycle of fruit growth, resulting in a large under-prediction of growth of this cohort. Apparently, the model gave first priority for assimilate to the first cohort to the detriment of the second cohort and later-set fruits. This simulated behavior was mostly confirmed because the simulated third cohort failed to start, in agreement with the observed failure of the third cohort to begin growth under N stress, even though these fruits were set and tagged. These late-set tiny fruits remained on the plant with no apparent growth until harvest.

Fruit dry matter concentration: Observed and simulated dry matter concentration in individual fruits from flowers which had been tagged at three weekly dates in plants grown under N stress are presented in Figures 7- 23 and 7-24. The model was able to mimic the decrease in dry matter concentration observed in fruits under N stress, compared to experimental results.

Simulated and measured data agreed reasonably well with a RMSE of 0.5 % and 0.9 % for cohorts 1 and 2, respectively. The desired variation in dry matter concentration was created by adding an NSTRES-dependent modifier to the equation that calculates the dry matter concentration for individual fruits (Eq. 7-6). Because the NSTRES signal itself is instantaneous (from today's N supply/N demand ratio), we used in equation 6-4 an 8-day running average (CNSTRES), which is a more cumulative memory type of variable, which worked well in this experiment. For this particular experiment, the N cutoff was permanent and no later N was applied, so the memory effect was not as critical. However, it would be appropriate to have a more cumulative signal (as was done for SWFAC) or running average to better account for the real response which is cumulative and to prevent sudden recovery in the event of late N fertilization for example.

Fruit fresh weight: Observed and simulated fresh weight accumulation in individual fruits from flowers that had been tagged at three weekly dates in plants under N stress is presented in Figures 7-24 and 7-25. There was good correspondence between simulated and observed data in case of cohort number 1. In these cohorts, the Willmott agreement index (d) was equal to 0.99 and the RMSE was 21 g which represents an error of 8 % of the single fruit final fresh weight. However the model underestimated the fresh mass toward the end of the season. Similar to dry weight prediction, a less satisfactory result occurred for cohort number 2. Cohort number 3 failed in the field and the crop model predicted failure for this cohort too.

Fruit size: Observed and simulated fruit diameter of individual fruits from flowers that had been tagged at three weekly dates in N stressed treatments is presented in Figures 7-27 and 7-28. Comparisons among cohorts showed that the fruit size of cohorts number 1 was well simulated by the model although size was underestimated toward the end of the season as a result

of the underestimation of fresh weight. The fruit size of cohort number 2 was poorly simulated because of the dependence of this variable on fresh mass and dry mass which as explained was poorly predicted for this cohort. To better simulate priorities among cohorts especially under N stress, there may be a need to modify code where the model currently gives a too strong (absolute) priority for the first cohort and lets the later ones fail. An alternative growth function could use Gompertz or logistic functions instead of the constant linear growth used by CROPGRO which would allow somewhat slower growth of cohorts number 1 and 2 late in their growth cycle, at a time when cohort number 3 could then begin growth sooner, particularly if the growth demand of that cohort is also in its slow growth phase (as represented in the Gompertz and logistics equations). These equations with slower growth demand early and late, may allow assimilate available to initiate growth of cohort 3 (later fruits). Another possibility is to allow partitioning to rise above XFRUIT late in the life cycle to carry the latest fruits, but these possibilities need be evaluated.

Conclusion

The CROPGRO-Tomato model was tested as a tool for predicting the dynamic growth of individual fruits and the whole plant when the crop was grown under water and N limitation. The effect of N supply, low leaf N concentration on photosynthesis, and the reducing factors SWFAC, TURFAC and NSTRES inside the CROPGRO model were suitable to reproduce efficiently reductions of whole plant growth and total fruit dry matter growth under N deficit. However, in this work, the same factors were then strategically connected to the addition and dry matter growth rate of individual fruits and the fruit's thermal time accumulator. In addition, these factors were used to modify the function that calculates the fruit dry matter concentration. The result was an improved ability of the model to mimic the dry weight and fresh weight growth and dry matter concentration behavior of individual fruits under stress. The results are promising and

suggest that the CROPGRO-Tomato model can be a useful research and application tool for tomato fruit yield and quality predictions. However, stress physiology in tomato fruits is complex and further experimental work is recommended in order to optimize the magnitude and timing of fruit growth when using SWFAC, TURFAC, and NSTRES as signals to affect the dynamics of tomato fruits under water and N stresses in the simulations.

Table 7-1. Physical, chemical and water holding capacity characteristics of soil series Tavares, (uncoated sand soil). Source Carlisle *et al.* (1988).

Layer cm	Lower limit	Upper limit	Soil Sat.	Root growth factor	K cm h^{-1}	Bulk density g cm^{-3}	Org. carbon %	pH water	Clay %	Silt %
5	0.072	0.142	0.364	1	21	1.6	1.41	4.2	1.5	1.5
15	0.072	0.142	0.364	1	21	1.6	1.41	4.2	1.5	1.5
30	0.051	0.102	0.371	0.638	21	1.6	0.66	4.3	1.5	1.2
45	0.044	0.091	0.371	0.472	21	1.6	0.44	4.3	1.5	1.5
60	0.045	0.092	0.347	0.350	21	1.6	0.18	4.2	1.3	1.5
90	0.038	0.078	0.35	0.223	21	1.67	0.18	4.2	1.5	1.5
120	0.046	0.086	0.364	0.122	21	1.63	0.08	4.3	3.0	1.2
150	0.048	0.087	0.365	0.067	21	1.63	0.08	4.4	4.0	1.5
180	0.052	0.091	0.358	0.037	21	1.65	0.05	5.0	5.0	1.5

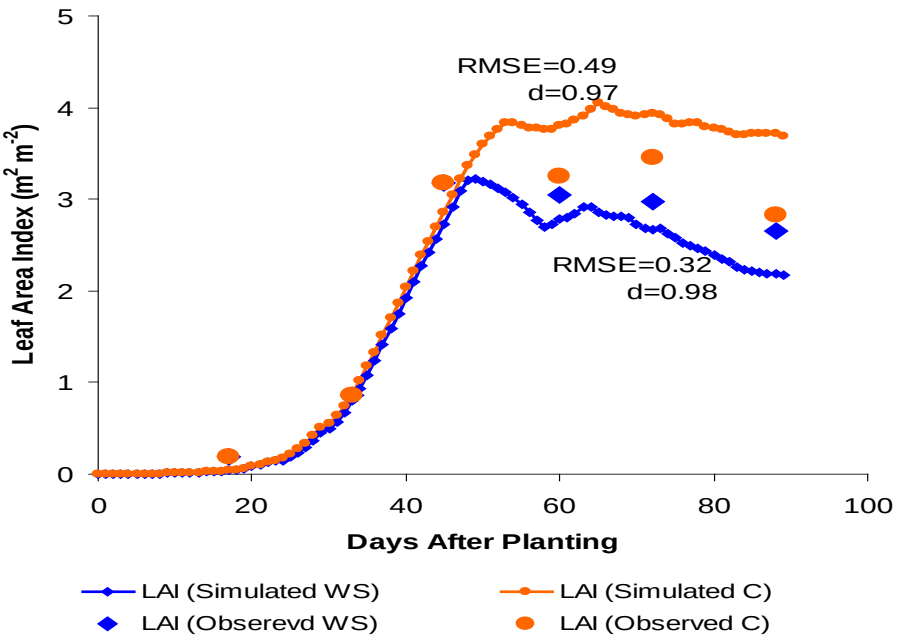

Figure 7-1. CROPGRO simulated (lines) and measured (points) leaf area index in Gainesville, FL during spring of 2007 comparing well irrigated with water stressed tomato plants.

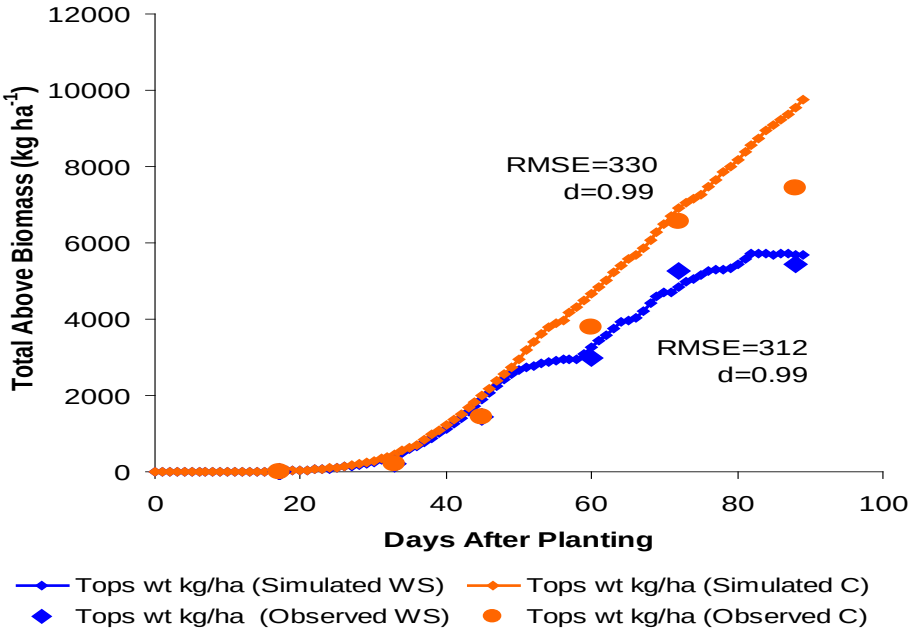

Figure 7-2. CROPGRO simulated (lines) and measured (points) total above biomass in Gainesville, FL during spring of 2007 comparing well irrigated with water stressed tomato plants.

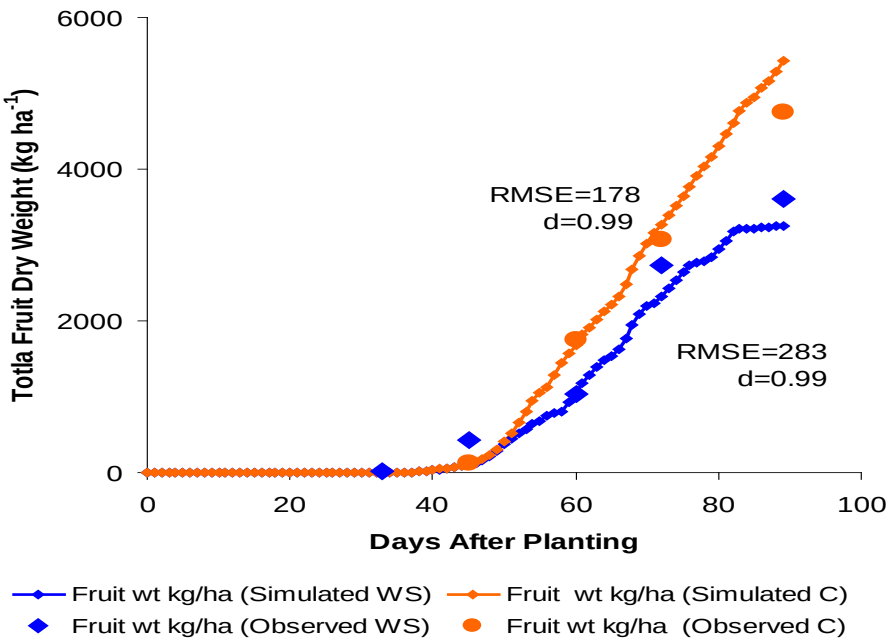

Figure 7-3. CROPGRO simulated (lines) and measured (points) total fruit dry weight in Gainesville, FL during spring of 2007 comparing well irrigated with water stressed tomato plants.

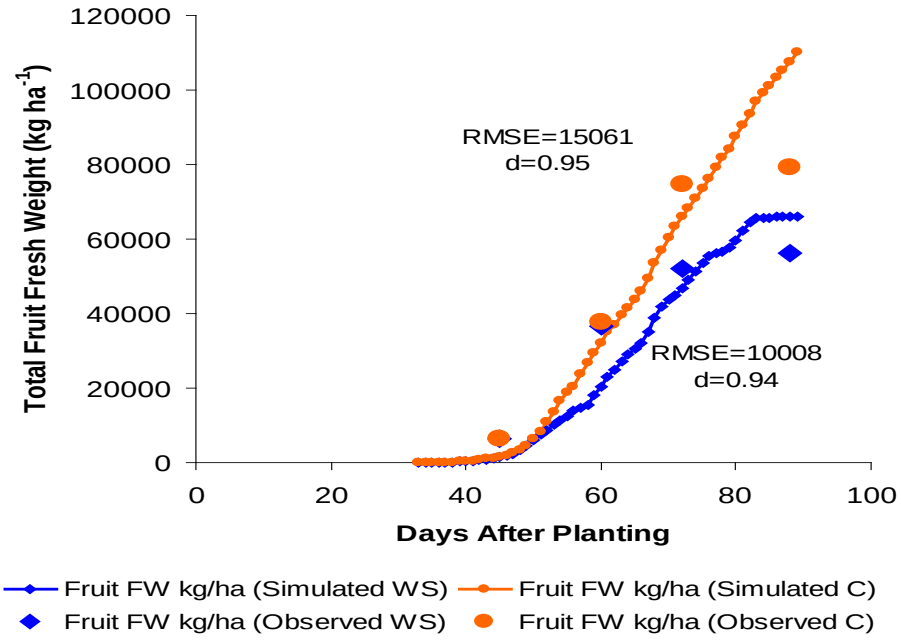

Figure 7-4. CROPGRO simulated (lines) and measured (points) total fruit fresh weight in Gainesville, FL during spring of 2007 comparing well irrigated with water stressed tomato plants.

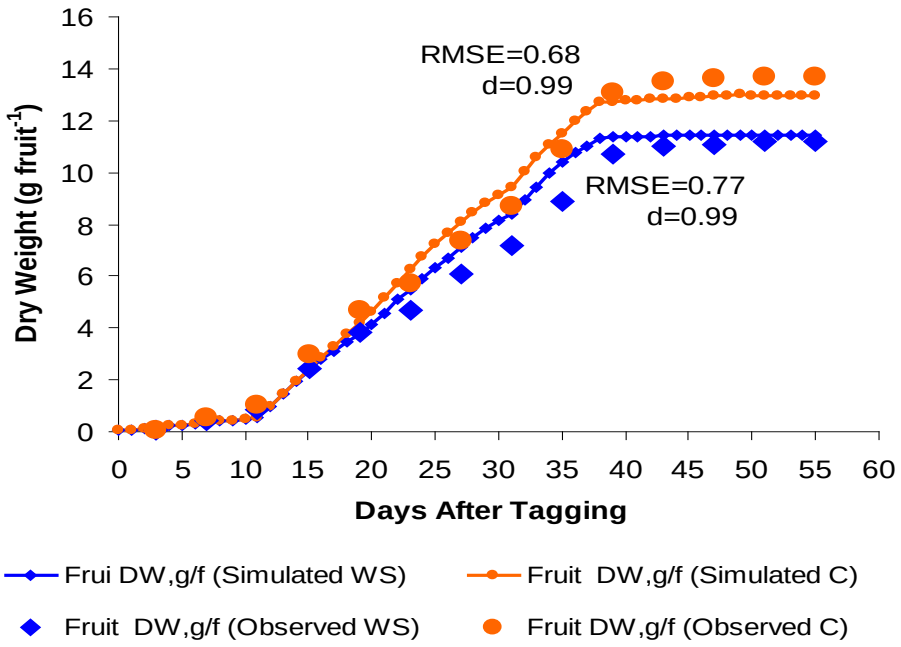

Figure 7-5. CROPGRO simulated (line) vs. observed (points) dry weight of individual fruits of cohort # 1 in Gainesville Fl, during spring 2007 comparing well irrigated with water stressed tomato plants.

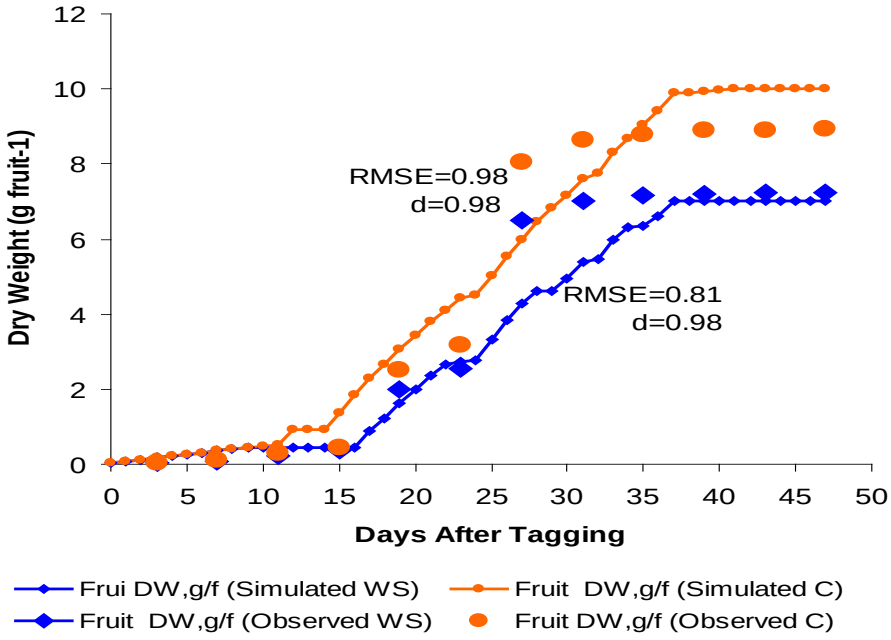

Figure 7-6. CROPGRO simulated (line) vs. observed (points) dry weight of individual fruits of cohort # 2 in Gainesville Fl, during spring 2007 comparing well irrigated with water stressed tomato plants.

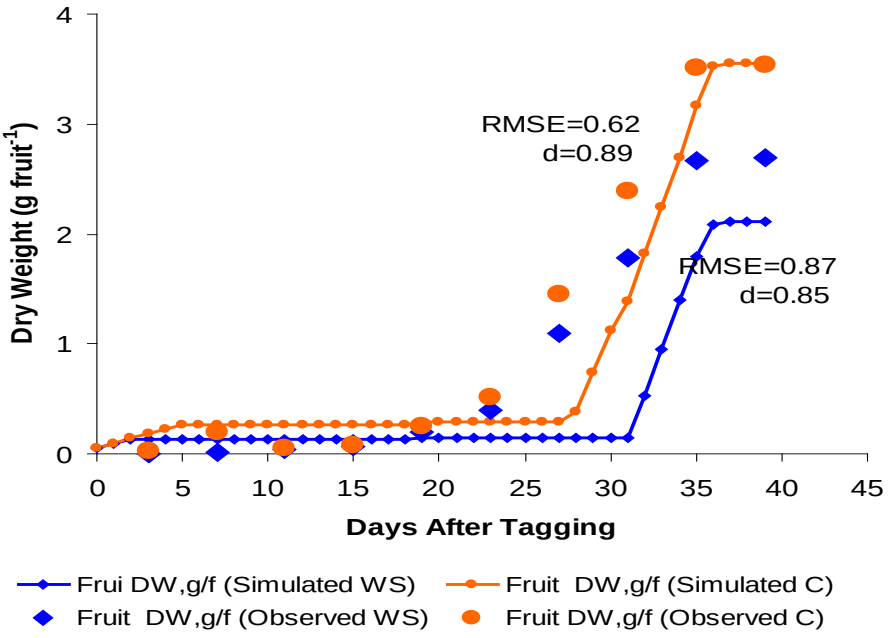

Figure 7-7. CROPGRO simulated (line) vs. observed (points) dry weight of individual fruits of cohort # 3 in Gainesville Fl, during spring 2007 comparing well irrigated with water stressed tomato plants.

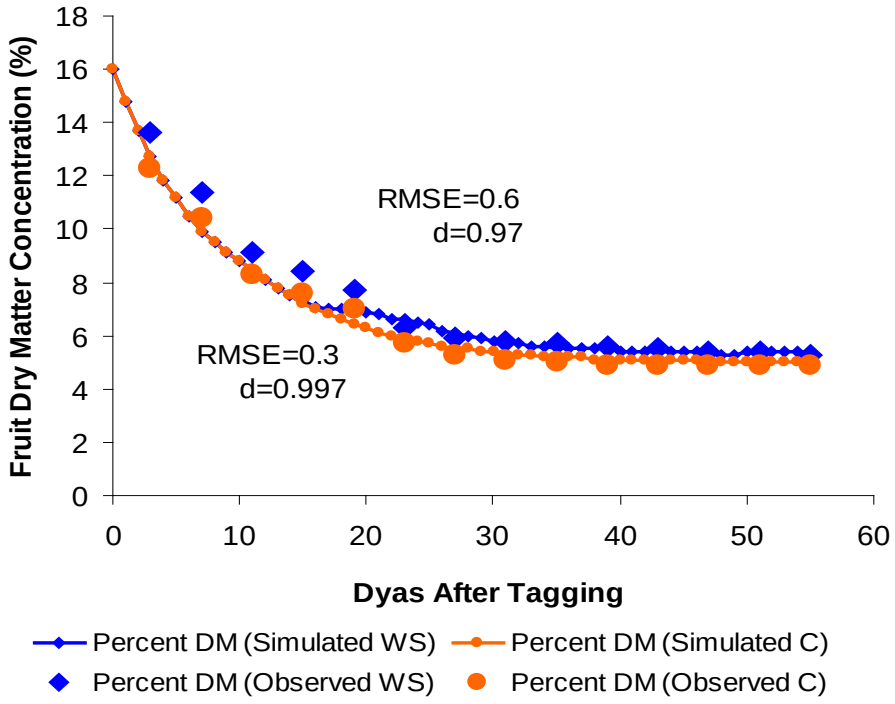

Figure 7-8. CROPGRO simulated (line) vs. observed (points) dry matter concentration of individual fruits of cohort # 1 in Gainesville Fl, during spring 2007 comparing well irrigated with water stressed tomato plants.

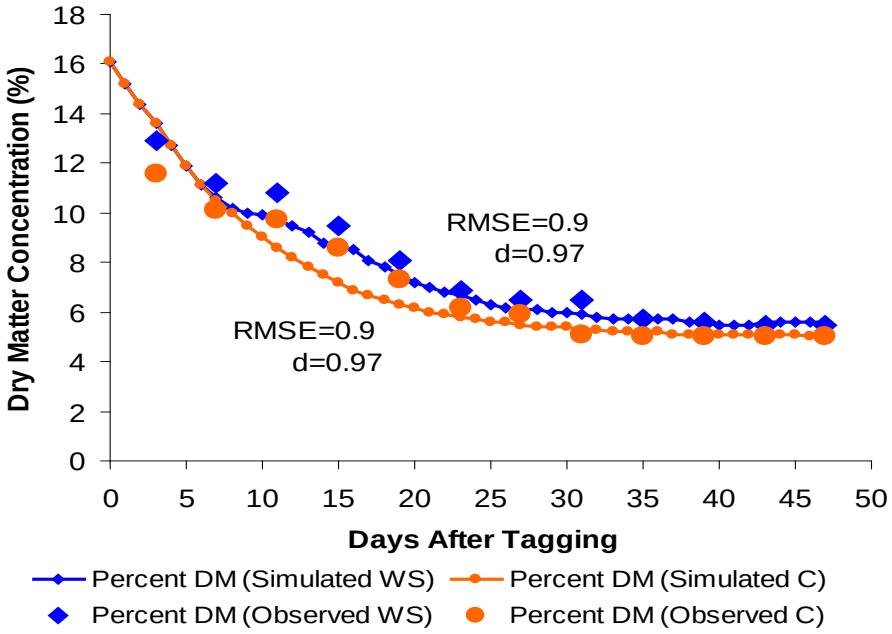

Figure 7-9. CROPGRO simulated (line) vs. observed (points) dry matter concentration of individual fruits of cohort # 2 in Gainesville Fl, during spring 2007 comparing well irrigated with water stressed tomato plants.

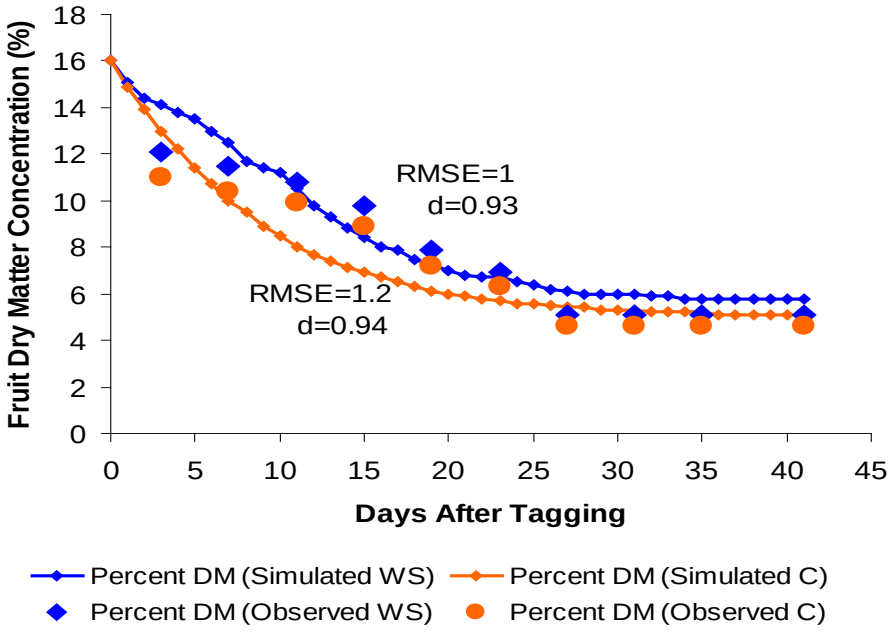

Figure 7-10. CROPGRO simulated (line) vs. observed (points) dry matter concentration of individual fruits of cohort # 3 in Gainesville Fl, during spring 2007 comparing well irrigated with water stressed tomato plants.

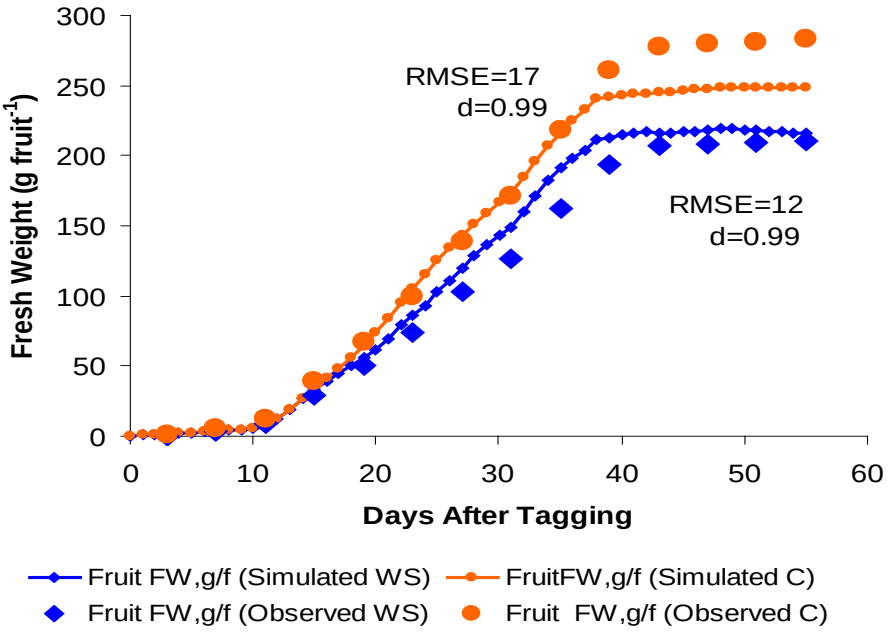

Figure 7-11. CROPGRO simulated (line) vs. observed (points) fresh weight of individual fruits of cohort # 1 in Gainesville Fl, during spring 2007 comparing well irrigated with water stressed tomato plants.

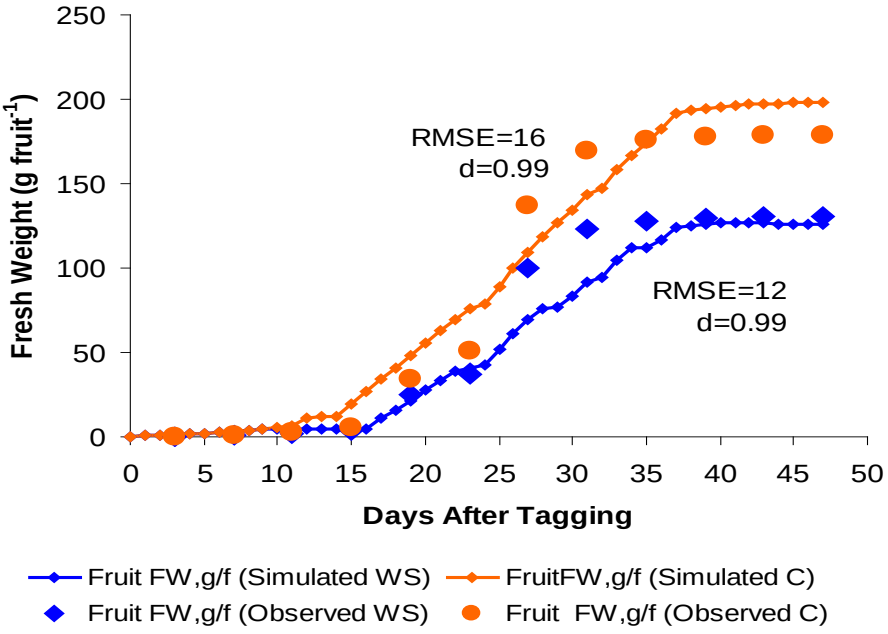

Figure 7-12. CROPGRO simulated (line) vs. observed (points) fresh weight of individual fruits of cohort # 2 in Gainesville Fl, during spring 2007 comparing well irrigated with water stressed plants.

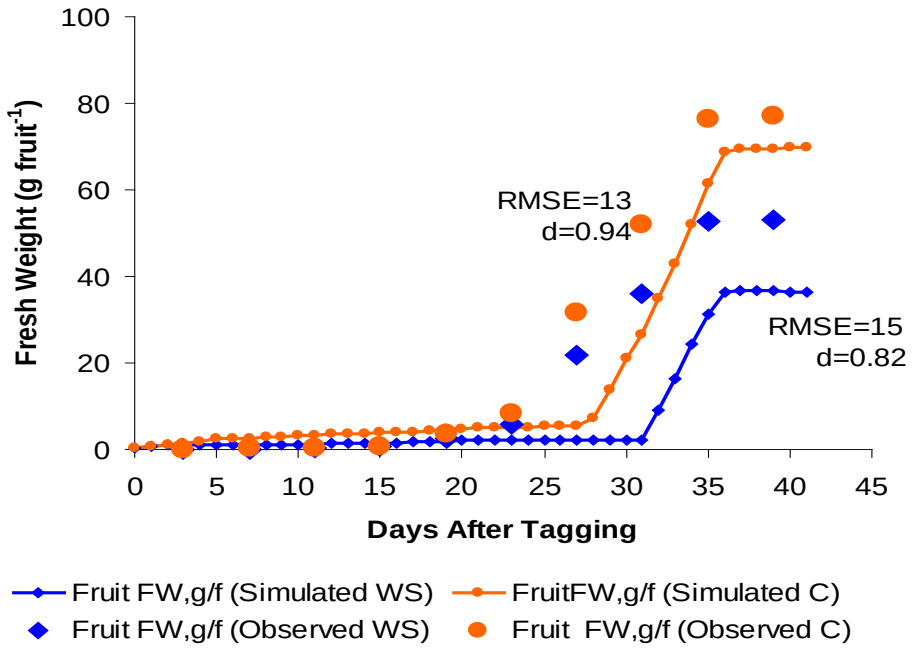

Figure 7-13. CROPGRO simulated (line) vs. observed (points) fresh weight of individual fruits of cohort # 3 in Gainesville Fl, during spring 2007 comparing well irrigated with water stressed tomato plants.

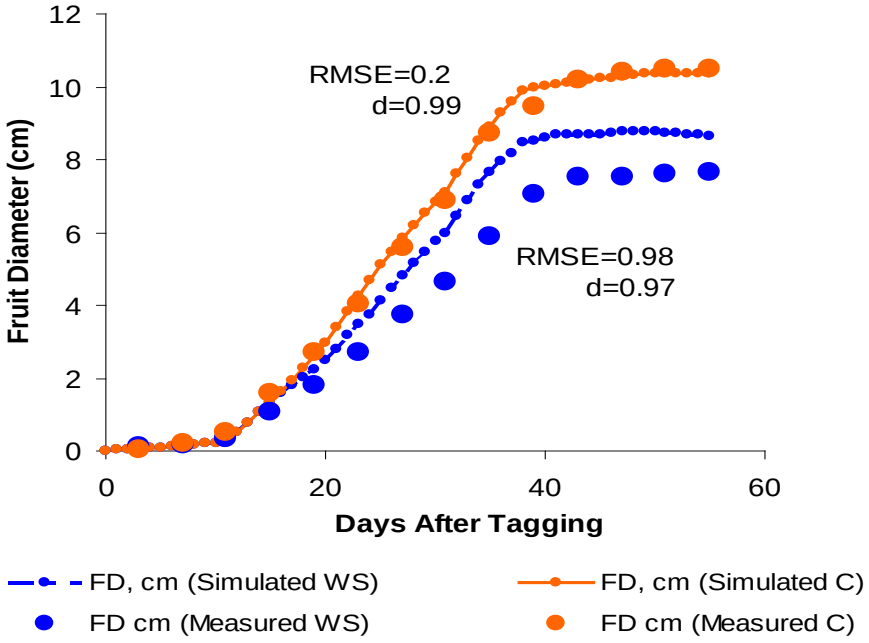

Figure 7-14. CROPGRO simulated (line) vs. observed (points) diameter of individual fruits of cohort # 1 in Gainesville Fl, during spring 2007 comparing well irrigated with water stressed tomato plants.

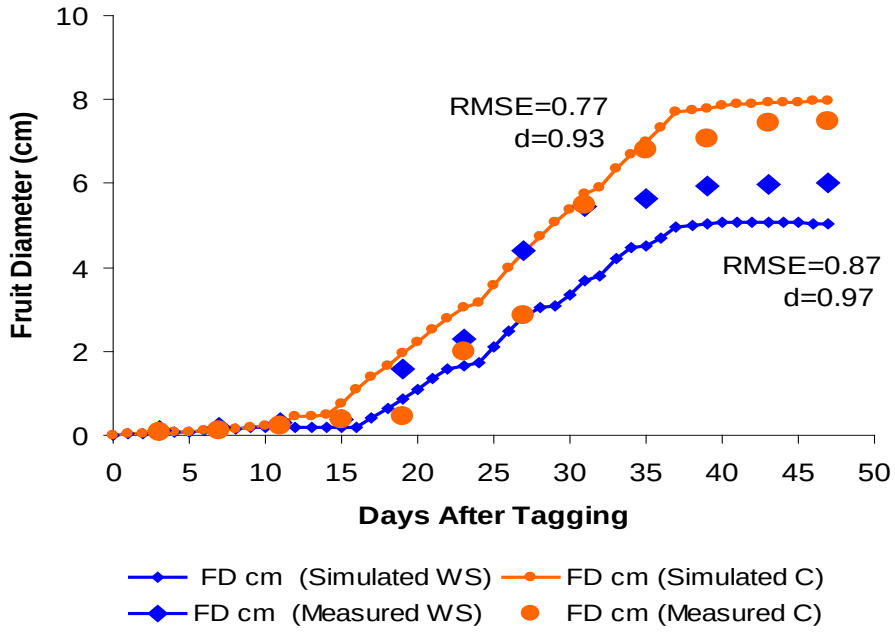

Figure 7-15. CROPGRO simulated (line) vs. observed (points) diameter of individual fruits of cohort # 2 in Gainesville Fl, during spring 2007 comparing well irrigated with water stressed tomato plants.

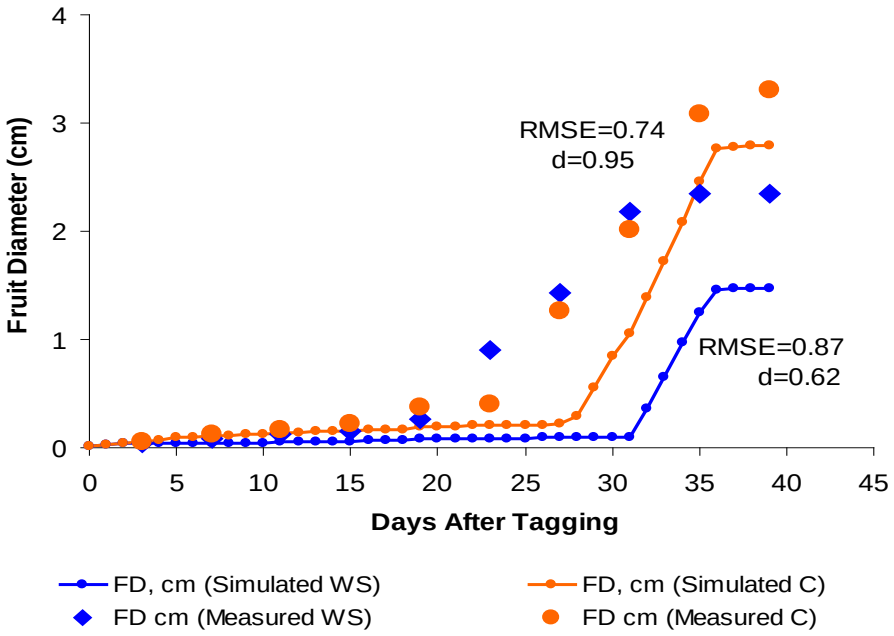

Figure 7-16. CROPGRO simulated (line) vs. observed (points) diameter of individual fruits of cohort # 3 in Gainesville Fl, during spring 2007 comparing well irrigated with water stressed tomato plants.

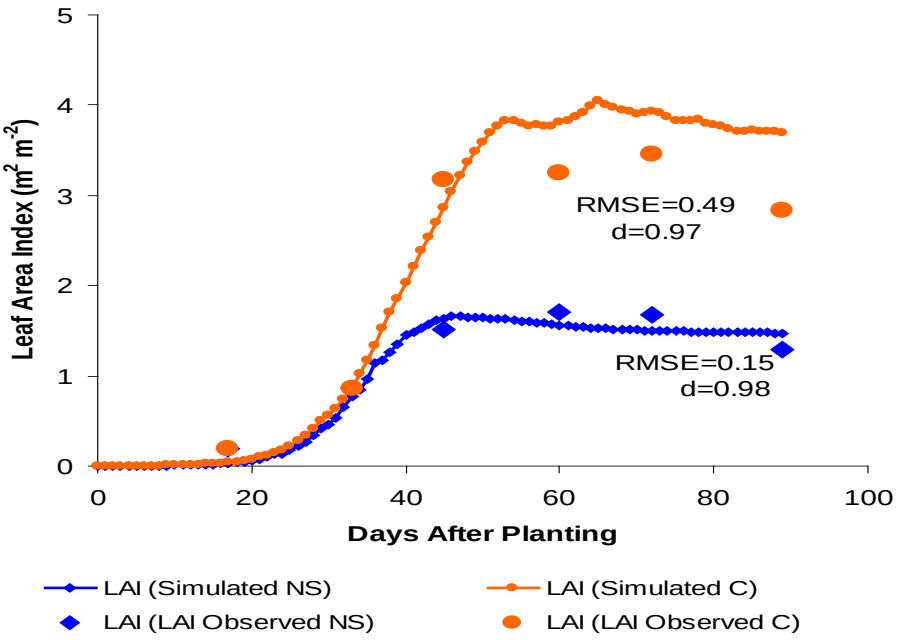

Figure 7-17. CROPGRO simulated (lines) and measured (points) leaf area index in Gainesville, FL during spring of 2007 comparing well fertilized with N stressed tomato plants.

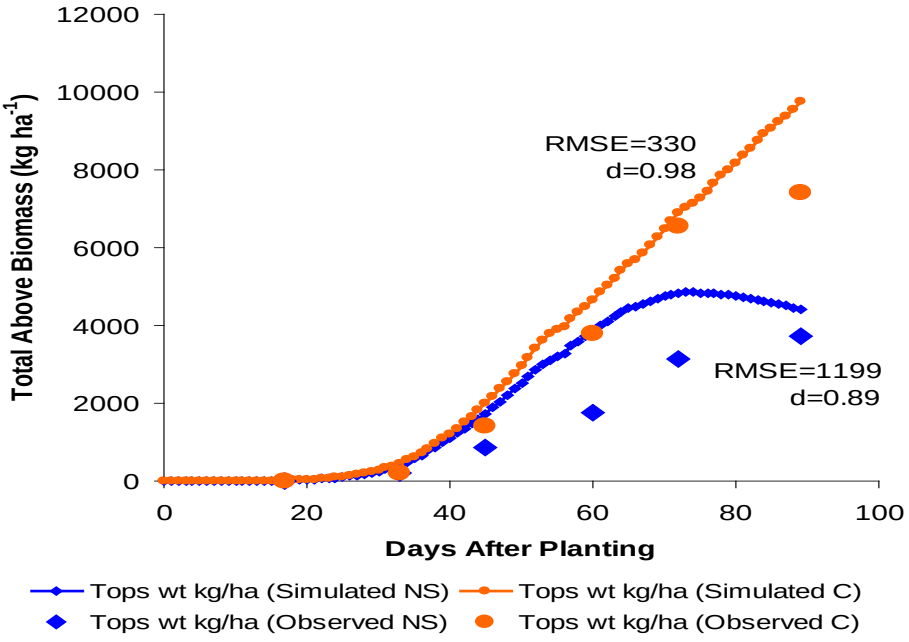

Figure 7-18. CROPGRO simulated (lines) and measured (points) above ground biomass in Gainesville, FL during spring of 2007 comparing well fertilized with N stressed tomato plants.

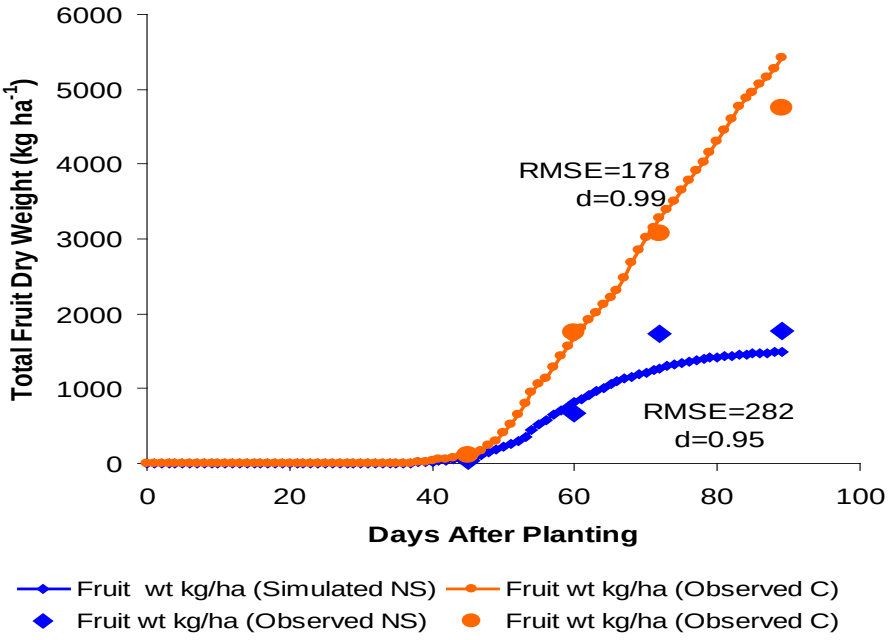

Figure 7-19. CROPGRO simulated (lines) and measured (points) total fruit dry weight in Gainesville, FL during spring of 2007 comparing well fertilized with N stressed tomato plants.

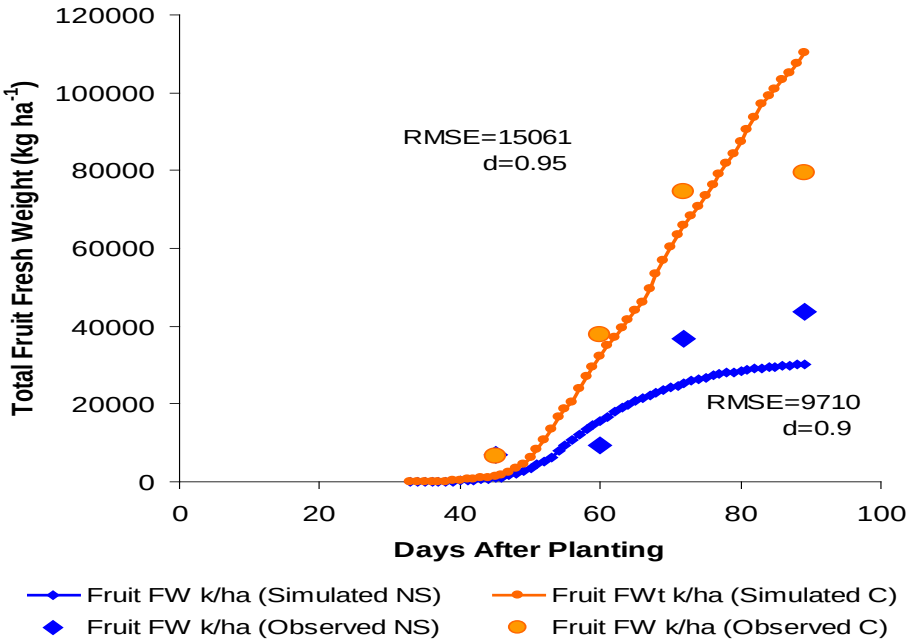

Figure 7-20. CROPGRO simulated (lines) and measured (points) total fruit fresh weight in Gainesville, FL during spring of 2007 comparing well fertilized with N stressed tomato plants.

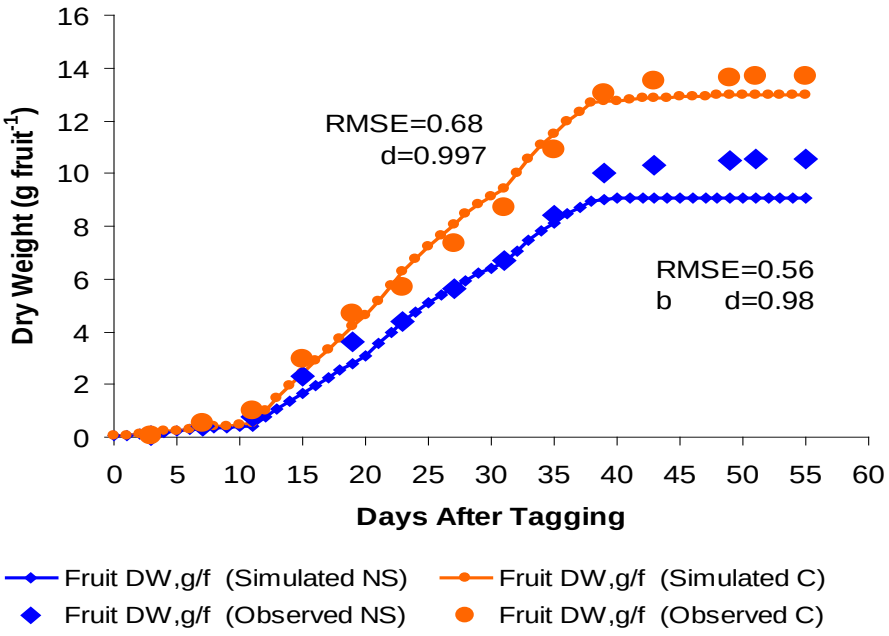

Figure 7-21. CROPGRO simulated (line) vs. observed (points) dry weight of individual fruits of cohort # 1 in Gainesville Fl, during spring 2007 comparing well fertilized with N stressed tomato plants.

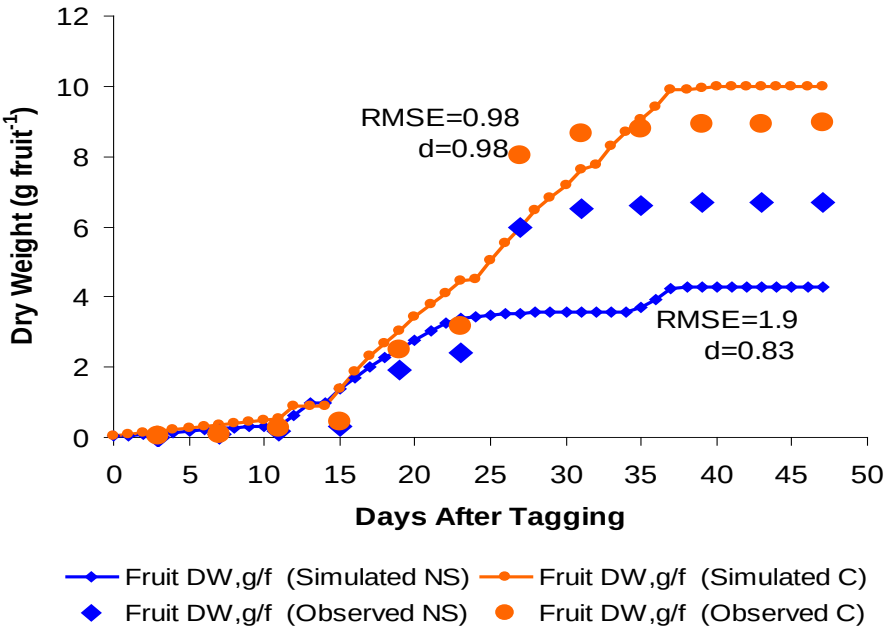

Figure 7-22. CROPGRO simulated (line) vs. observed (points) dry weight of individual fruits of cohort # 2 in Gainesville Fl, during spring 2007 comparing well fertilized with N stressed tomato plants.

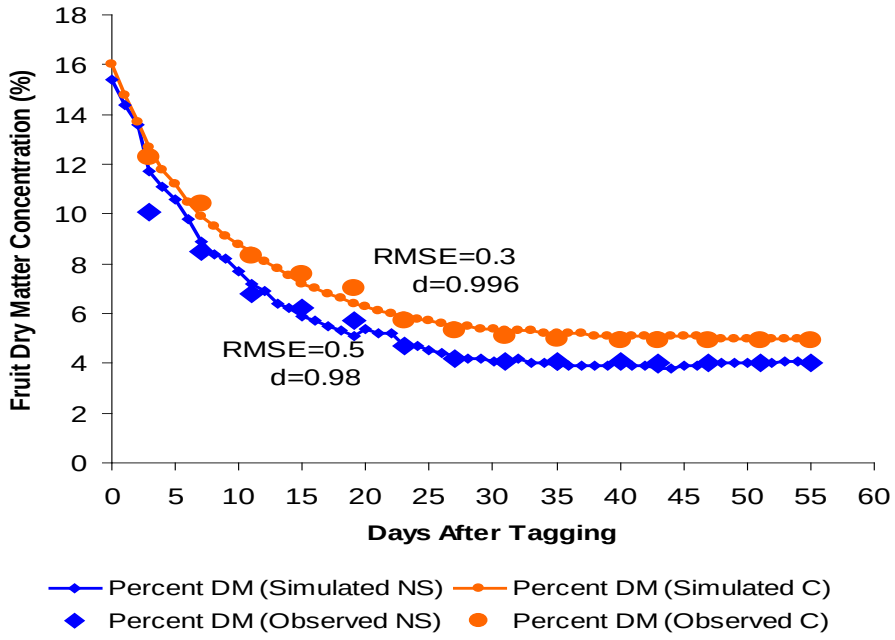

Figure 7-23. CROPGRO simulated (line) vs. observed (points) dry matter concentration of individual fruits of cohort # 1 in Gainesville Fl, during spring 2007 comparing well fertilized with N stressed tomato plants.

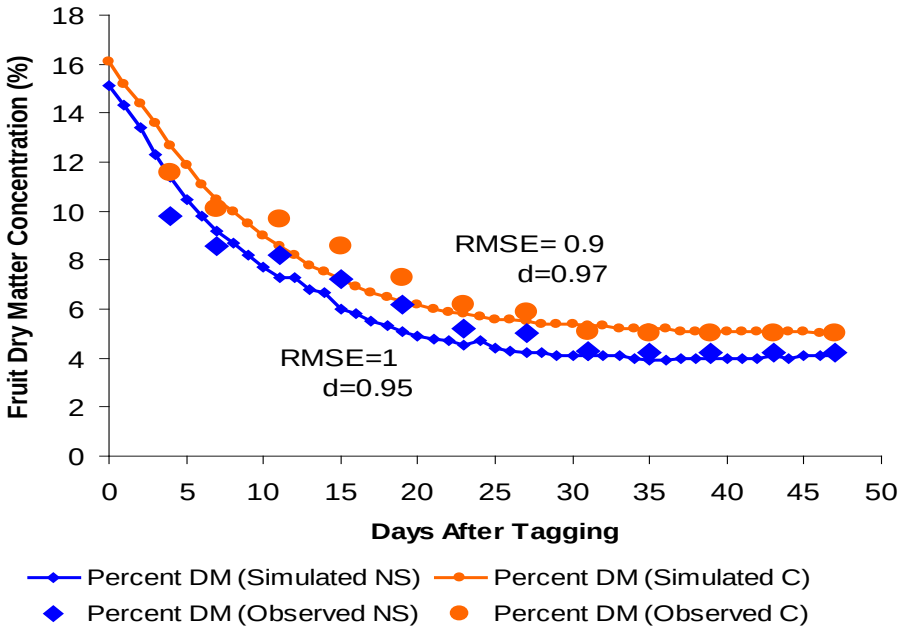

Figure 7-24. CROPGRO simulated (line) vs. observed (points) dry matter concentration of individual fruits of cohort # 2 in Gainesville Fl, during spring 2007 comparing well fertilized with N stressed tomato plants.

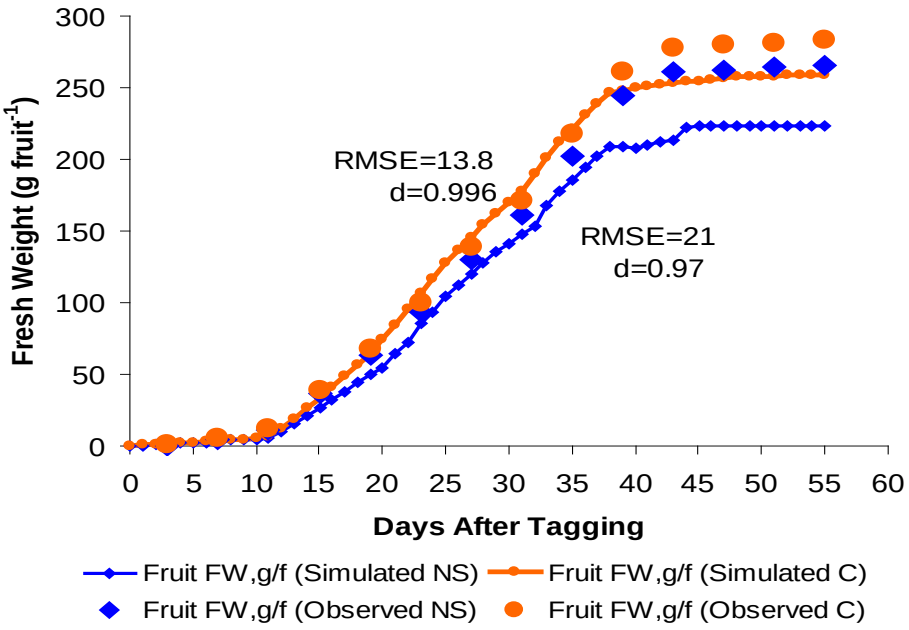

Figure 7- 25. CROPGRO simulated (line) vs. observed (points) fresh weight of individual fruits of cohort # 1 in Gainesville Fl, during spring 2007 comparing well fertilized with N stressed tomato plants.

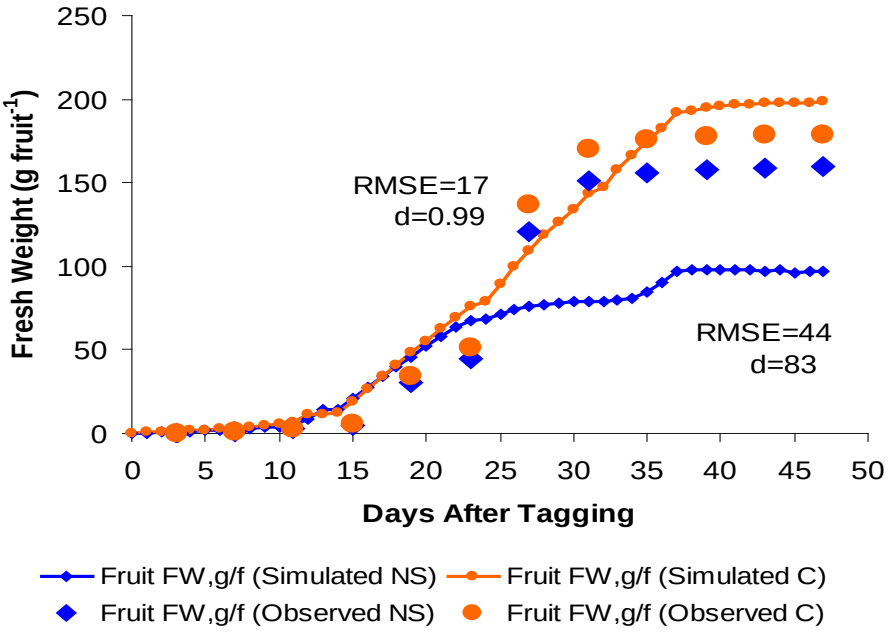

Figure 7-26. CROPGRO simulated (line) vs. observed (points) fresh weight of individual fruits of cohort # 2 in Gainesville Fl, during spring 2007 comparing well fertilized with N stressed tomato plants.

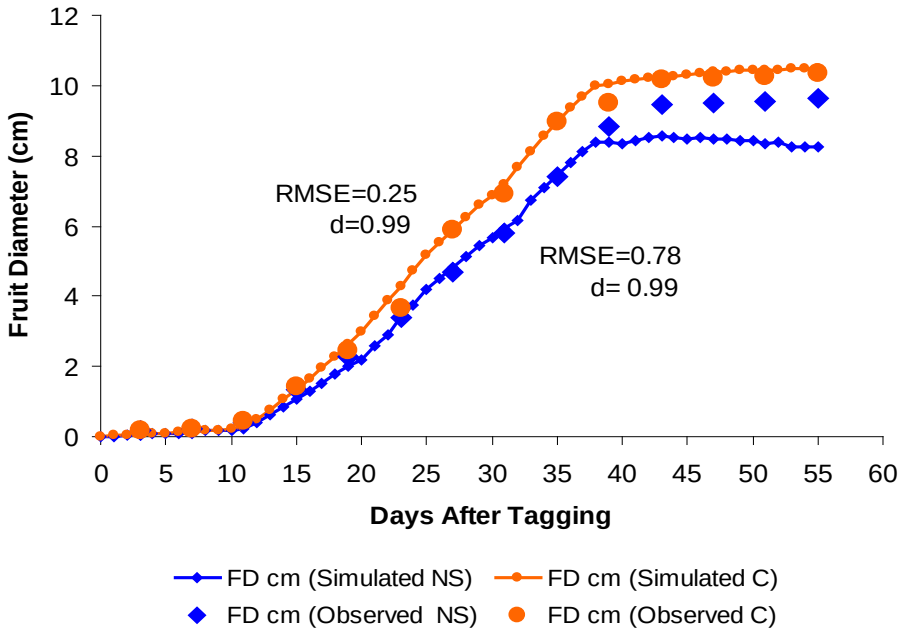

Figure 7-27. CROPGRO simulated (line) vs. observed (points) diameter of individual fruits of cohort # 1 in Gainesville Fl, during spring 2007 comparing well fertilized with N stressed plants.

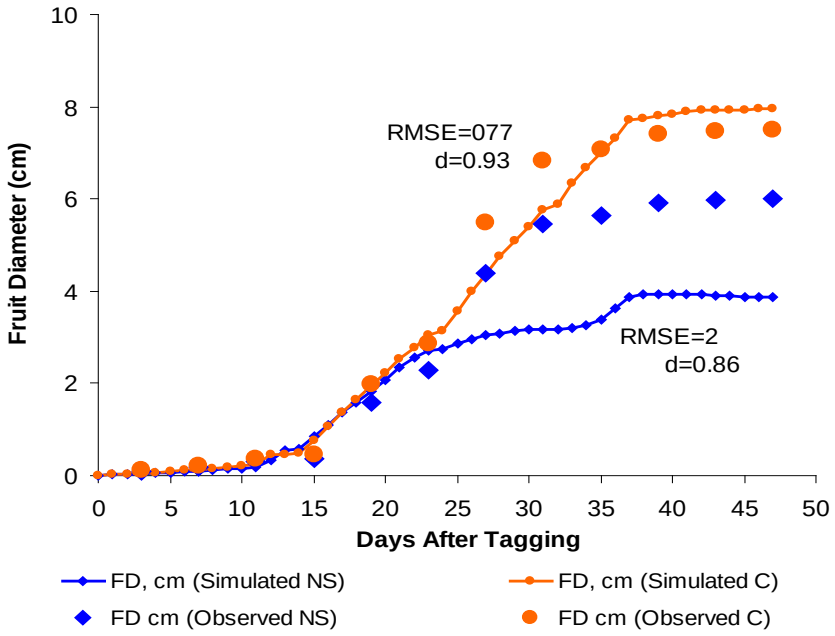

Figure 7-28. CROPGRO simulated (line) vs. observed (points) diameter of individual fruits of cohort # 2 in Gainesville Fl, during spring 2007 comparing well fertilized with N stressed plants.

CHAPTER 8
CONCLUSIONS

One important feature of CROPGRO is the generic nature of the model that allows many applications around the world where model users work with different cultivars at different locations and during different seasons. That is possible because the main processes and functions are common for most the species, a fact that is implicit in the modular structure of CROPGRO. Therefore, CROPGRO simulations are good as long as the model is correctly calibrated according to genotypes, and soils and climates are accurately input. The calibration processes are more easy and efficient if the genetics parameters of the model are the correct for the specie. CROPGRO-tomato was developed more than 10 years ago and until now has not been modified. We found literature, published after the model was developed, that suggests that the values of the cardinal temperature that control the plant phenology might need adjustments. Therefore, in this work we updated the cardinal temperatures for tomato phenology (vegetative development, early reproductive growth and late reproductive growth). Cardinal temperatures for fruit set and pollination and fruit growth were updated as well. Most of the time the cardinal temperatures were reduced compared to the prior default version of the model by 2°C to 4°C depending on the plant phenological phase. We re-calibrated the model according to these updates using nine experimental data sets. Overall the performance of the model for simulating total biomass and fruit dry weight yield was improved after the updates and re-calibration. Because the new values of temperature coefficients came from experiments conducted in environments with controlled temperature, we think that the cardinal temperatures for phenology, fruit setting and growth of tomato should be updated in the current version of CROPGRO- tomato.

When tomato is produced for fresh market, the ability to control fruit fresh weight and size during the life cycle may have economic benefits because these are the variables that affect most

the yield and price of the production. Crop models are valuable tools to understand the main factors causing variability on these attributes as well as for predicting the harvest window. Often the later goal is the larger concern of growers who want to plan efficiently their crop according to when they will have the best chance to obtain better prices. However, most of models developed for tomato lack the ability to predict fruit growth in terms of fresh mass and marketable size, and are limited to predictions of yield as total fruit dry weight. The most recent version of CROPGRO-tomato (not yet released) includes a subroutine for dynamically simulating the fruit growth in terms of fresh weight, dry matter concentration, and fruit size distribution. The most important part of this work is that we re-calibrated this new feature of the model and successfully evaluated the quality of the simulations with independent data. This is the first report of validation of single fruit fresh weight and size and we found that the model was able to simulate reasonably well the fruit growth in terms of dry weight and fresh weight, dry matter concentration and size of individual fruits initiated on different dates (three fruit ages spaced one week apart). In agreement with the observations and supported by literature, the model revealed that the growth of the fruit is strongly related to the initiation date, with earlier set fruits having higher sink strength than the later set fruits. The model error averaged for all cohorts and variables was less than 20 % and the values of d index always was above 0.95, showing the suitability of the model for prediction over time.

In order to assess whether stress conditions produce variations in the growth of individual fruits, we grew tomato plants under water and nitrogen stress conditions and evaluated the growth of single fruits over time. We found that both stresses caused differences in the fruit growth behavior. N stress affected mainly the dry matter accumulation while fresh weight and fruit size were quantitatively less affected. The water stress treatment, on other hand, produced

smaller fruits that accumulated less fresh mass than well-irrigated fruits. Contrary to N results, the dry weight of fruits under water stress was less affected and because of the reduction in size and fresh mass, the dry matter concentration of these fruits increased. Leaf photosynthesis rate was reduced and the stomatal resistance was increased in plants under stress, thus contributing to the mass reduction. The partitioning of dry matter toward fruits was not affected under water stress but it was reduced under N stress.

CROPGRO-tomato has several functions that allow simulating the effect of different stresses at the whole plant level. After analyzing how the growth of individual fruit was affected by water and N stress, the next step was to evaluate if the stress functions in CROPGRO-tomato model could predict the growth of individual fruits under stress. Stress factors such as SWFAC and TURFAC (for water stress) and NSTRES (for N stress), which are efficient to mimic stress at a whole plant level, were strategically connected to functions of fruit growth in the code in order to affect the timing (thermal time accumulator), the rate of single fruit growth as well as the dry matter concentration. We obtained a good response of the model in simulating water stress effects but more work needs to be done in order to make the model better predict N stress where simulated effects were stronger than we observed in our experiments.

LIST OF REFERENCES

Abreu P, Meneses JF, Gary C. 2000. Tompousse, a model of yield prediction for tomato crops: Calibration study for unheated plastic greenhouse. *Acta Horticulturae* **519**, 141-149.

Acock B, Edwards CDA, Fitter DJ, Hand DW, Ludwing LJ, Warren WJ, Withers AC. 1978. The contribution of leaves from different levels within a tomato crop to canopy net photosynthesis: An experimental examination of two canopy models. *Journal of Experimental Botany* **29**, 815-827.

Acock B, Reynolds JF. 1989. The rationale for adopting a modular generic structure for crop simulators. *Acta Horticulturae* **284**, 391-396.

Acock B. 1991. Modelling canopy photosynthesis response to carbon dioxide, light interception, temperature and leaf traits. In: Boote KJ, Loomis RS, eds. *Modeling crop photosynthesis from biochemistry to canopy*. American Society of Agronomy, Madison, WI, pp 41-55.

Adams P. 1986. Mineral Nutrition. In: Atherton, JG, Rudich, J, eds. *The tomato crop. A scientific basis for improvement*. London: Chapman & Hall, pp 281-334.

Adams SR, Valdez VM, Cave CRJ, Fenlon JS. 2001a. The impact of changing light levels and fruit load on the pattern of tomato yields. *Journal of Horticultural Science and Biotechnology* **76**, 368-373.

Adams SR, Cockshull KE, Cave CRJ. 2001b. Effect of temperature on the growth and development of tomato fruits. *Annals of Botany* **88**, 869 -877.

Adams SR, Valdez VM. 2002. The effect of periods of high temperature and manipulating fruit load on the pattern of tomato yields. *Journal of Horticultural Science* **77**, 461- 466.

Aikman DP. 1989. Potential increase in photosynthetic efficiency from the redistribution of solar radiation in a crop. *Journal of Experimental Botany* **40**, 855-864.

Aikman DP. 1996. A procedure for optimizing carbon dioxide enrichment of a glasshouse tomato crop. *Journal of Agricultural Engineering* **63**, 171-184.

Akaki T, Eguchi T, Wajima T, Yoshida S, Kitano M. 2004. Dynamic analysis of growth, water balance and sap fluxes through phloem and xylem in a tomato fruit: short term effect of water stress. *Environment Control in Biology* **42**(3), 225-240.

A**larcon JJ, Sanchez Blanco MJ, Bolarin MC, Torrecillas A**. 1994. Growth and osmotic adjustment of two tomato cultivars during and after saline stress. *Plant and Soil* **166**, 75-82.

Alian A, Altman A, Heuer B. 2000. Genotypic differences in salinity and water stress tolerance of fresh market tomato cultivars. *Plant Science* **152**, 59 -65.

Atherton JG, Rudich J. 1986. *The tomato crop. A scientific basis for improvement*. London: Chapman and Hall. 221 - 234.

Atherton JG, Harris GP. 1986. Flowering. In: Atherton JG, Rudich J, eds. *The tomato crop. A scientific basis for improvement*. New York: Chapman & Hall, pp 167- 200.

Aung LH. 1978. Temperature regulation of growth and development of tomato during ontogeny. In: Cowell R, ed. *Proceedings of the 1st International Symposium on Tropical Tomato*. Asian Vegetable Research and Development Center Publication no. 78-59, Shanhua, Taiwan, Republic of China, 79 - 93.

Bailey BJ, Hunter A. 1988. Plant response and energy use in five high thermal resistance greenhouses. *Acta Horticuturae* **229**, 165-171.

Bangerth F, Ho LC. 1984. Fruit position and fruit set sequence in a truss as factors determining final size of tomato fruits. *Annals of Botany* **53**, 315-319.

Barker AV, Mills HA. 1980. Ammonium and nitrate nutrition of horticultural crops. In: Janick J, ed. *Horticultural Reviews*, Westport, CT; AVI Publishing, pp 395-423.

Bar-Tal A, Keinam M, Fishman S, Aloni B, Oserovitz Y, Genard M. 1999. Simulation of environmental effects on Ca content in pepper fruit. *Acta Horticulturae* **507**, 253-262.

Benedictos PJr, Yavari N. 2000. Optimum sowing date in relation to flower drop reduction in tomato. *Acta Horticulturae* **533**, 351-357.

Berman ME, Dejong TM. 1996. Water stress and crop load effects on fruit fresh and dry weight in peach (*Prunus persica*). *Tree Physiology* **16**, 859-864.

Bernacchi D, Beck-Bunn T, Eshed Y, Lopez Y, Petiard V, Uhlig J, Zamir D, Tanksley S. 1998. Advances backcross QTL-analysis in tomato. Identification of QTLs for traits of agronomic importance from *Lycopersicon hirsutum*. *Theoretical and Applied Genetic* **97**, 381-397.

Bertin N, Gary C. 1992. Tomato fruit set competition for assimilates, during the early production period. *Acta Horticulturae* **303**, 121-126.

Bertin N. 1993. Environnement climatique, competition pour les assimilats et modélisation de la nouaison de la tomate en culture sous serre. Thèse (Doctorat), Institut National Agronomique Paris-Grignon, Paris.

Bertin N, Heuvelink E. 1994. Dry matter production in a tomato crop: comparison of two simulaton models. *Journal of Horticultural Science* **68**, 995-1011.

Bertin N. 1995. Competition for assimilates and fruit position affect fruit set in indeterminate greenhouse tomato. *Annals of Botany* **75**, 55-65.

Bertin N, Gary C. 1998. Short and long term fluctuations of the leaf mass per area of tomato plants. Implications for growth models. *Annals of Botany* **82**, 71-81.

Bertin N, Gary C, Tchamitchian M, Vassiere BE. 1998. Influence of cultivar, fruit position and seed content on tomato fruit weight during crop cycle under low and high competition for assimilates. *Journal of Horticultural Science and Biotechnology* **73**(4), 541-548.

Bertin N, Buret M, Gary C. 2001. Insights into formation of tomato quality during fruit development. *Journal of Horticultural Science and Biotechnology* **76** (6), 786-792.

Bertin N, Genard M, Fishman S. 2003. A model for an early stage of tomato fruit development: cell multiplication and cessation of the cell proliferative activity. *Annals of Botany* **92**, 67-72.

Bertin N. 2005. Analysis of the tomato fruit growth response to temperature and plant fruit load in relation to cell division, cell expansion and DNA endoreduplication. *Annals of Botany* **95**, 439-447.

Bertin N, Causse M, Brunel B, Tricon D, Genard M. 2008. Identification of growth processes involved in QTLs for tomato fruit size and composition. *Journal of Experimental Botany* Advance Access published November 2008. 1-12.

Bohner J, Bangerth F. 1988. Effects of fruit set sequence and defoliation on cell number, cell size and hormone levels of tomato fruits (*Lycopersicon eculentum* Mill.) within a truss. *Journal of Plant Growth Regulation* **7**, 141-155.

Bohner J, Hedden P, Bora-Haber E, Bangerth F. 1988. Identification and quantification of gibberellins in fruits of *Lycopersicon esculentum*, and their relationship to fruit size in *L. esculentum* and *L. pimpinellifolium*. *Physiologia Plantarum* **73**, 348-353.

Boote KJ, Pickering NB. 1994. Modeling photosynthesis of row crop canopies. *Hortscience* **29,** 1423-1434.

Boote KJ, Jones JW, Hoogenboom G, Pickering NB. 1998. The CROPGRO model for grain legumes. In: Tsuji GY, Hoogenboom G, Thornton PK, eds. *Understanding Options for Agricultural Production*. Dordrecht: Kluwer Academic Publishers, pp 99-128.

Boote KJ, Jones JW, Hoogenboom G, Batchelor WD, Porter CH. 2000. CROPGRO plant growth and partitioning module. In DSSAT v. 4.0. Documentation and source code listing. Research Report Number **2000-1204**. University of Florida, Gainesville Fl.

Boote, KJ, Minguez MI, Sau F. 2002. Adapting the CROPGRO legume model to simulate growth of faba bean. *Agronomy Journal* **94**, 743-756.

Boote, KJ, Scholberg JMS. 2006. Developing, parameterizing and testing of dynamic crop growth models for horticultural crops. *Acta Horticulturae **718***, 23-34.

Bournival BL, Vallejos CE , Scott JW. 1990. Genetic analysis of resistances to races 1 and 2 of *Fusarium oxisporum* f. sp. *Lycopersici* from the wild tomato *Lycopersicon pennellii*. *Theoretical and Applied Genetic* **79**, 641-645.

Bremer JM, Mulvaney CS. 1982. Nitrogen-total. In: Black ed. *Methods of soil analysis* (2nd ed.), *Agronomy Monograph* **vol. 9** Part 2. Madison, WI, pp. 595-622.

Bruchou C, Genard M. 1999. A space time model of carbon translocation along a shoot bearing fruits. *Annals of Botany* **84**, 565-576.

Bruggink GT, Heuvelink E. 1987. Influence of light on the growth of young tomato, cucumber and sweet pepper plants in the greenhouse: effects on relative growth rate, net assimilation rate and leaf area ratio. *Scientia Horticulturae* **31**, 161-174.

Bussieres P. 1993. Potential dry matter and water import rates in the tomato fruit in relation to fruit size. *Annals of Botany* **72**, 63-72.

Bussieres P. 1994. Water import rate in tomato fruit: A model of resistance. *Annals of Botany* ***73***, 75**-**82.

Buster TP. 1979. Soil survey of Marion County, Florida. Soil Conservation Service, Washington, D.C. 1979.

Calado AM, Portas CAM. 1980. Growth and development of tomato *'Cal j'*. *Acta Horticulturae* **100**, 159-168.

Calado AM, Portas CAM. 1987. Base temperature and date of planting in processing tomatoes. *Acta Horticulturae* **200**, 185-193.

Calvert A. 1957. Effect of the early environment on the development of flowering in the tomato. I. Temperature. *Journal of Horticultural Science* **32**, 9-17.

Castrillo M, Fernandez D, Calcagno AM, Trujillo I, Guenni L. 2001. Response of Ribulose-1,5-bisphosphate carboxylase, protein content, and stomatal conductance to water deficit in maize, tomato, and bean. *Photosynthetica* **39** (2), 221-226.

Carlisle VW, Sodek FIII, Collins ME, Hammond LC, Harris WG. 1988. Characterization data for selected Florida soils. University of Florida Institute of Food and Agricultural Sciences, Soil Science Research Report **88-1**, Gainesville, FL. 28-249.

Causse M, Saliba Colombani V, Lecomte L, Duffe P, Rouselle P, Buret M. 2002. QTL analysis of fruit quality in fresh market tomato: a few chromosome regions control the variation of sensory and instrumental traits. *Journal of Experimental Botany* **377** (53), 2089-2098.

Cleary B, Laerr J, Hamel J. 1996. Guidelines for measuring plant moisture stress with a pressure chamber. PMS Instrument Co. 480 SW, Airport Avenue Corvallis, Albany OR, USA.

Cockshull KE. 1988. The integration of plant physiology with physical changes in the greenhouse climate. *Acta Horticulturae* **229**, 113-123.

Cockshull KE, Ho LC. 1995. Regulation of tomato fruit size by plant density and truss thinning. *Journal of Horticultural Science* **70**, 395-407.

Cockshull KE, Graves CJ, Cave CRJ. 1992. The influence of shading on yield of glasshouse tomatoes. *Journal of Horticultural Science* **67**, 11-24.

Coombe B. 1976. The development of fleshy fruits. *Annual Review of Plant Physiology* **27**, 207-228.

Cuartero J, Fernandez Munoz R. 1999. Tomato and salinity. *Scientia Horticulturae* **78**, 83-125.

Challa H, Heuvelink E, Van Meeteren U. 1995. Crop growth and development In: Bakker JC, Le Bot GPA, Challa H,Van de Braak NJ, eds. *Greenhouse climate control an integral approach*. Wageningen: Wageningen Press, pp 62-84.

Challa H, Bakker J. 1998. Potential production within the greenhouse environment. In: Enoch Z, Stanhill G, eds. Ecosystems of the world. *The greenhouse ecosystem*. Amsterdan: Elsevier, pp 333-348.

Chamarro JC. 1995. Anatomia y fisiologia de la planta. In: Nuez F, ed. *El cultivo del Tomate*. Madrid: Mundi Prensa, pp 201-239.

Charles WB, Harris, RE. 1972. Tomato fruit-set at high and low temperatures. *Canadian Journal of Plant Science* **52**, 497-506.

Davies JN, Hobson GE. 1981. The constituents of tomato fruits the influence of the environment, nutrition and genotype. CRC *Critical Reviews in Food Science and Nutrition* **15**, 205-280.

De Koning, ANM. 1989a. Development and growth of a commercially grown tomato crop. *Acta Horticulturae* **260**, 267-270.

De Koning ANM. 1989b. The effect of the temperature on fruit growth and fruit load of tomato. *Acta Horticulturae* **248**, 329-336.

De Koning ANM. 1990. Long term temperature integration of tomato. Growth and development under alternating temperature regimes. *Scientia Horticulturae* **45** 117-127.

De Koning ANM, De Ruiter HW. 1991. Effect of temperature, plant density and fruit thinning on flower/fruit abortion and dry matter partitioning of tomato. Annual Report **1990**. Glasshouse Crops Research Station, Naaldwijk, The Netherlands, 29.

De Koning ANM. 1993. Growth of tomato crop: measurements for crop model validation. *Acta Horticulturae* **328**, 141-146.

De Koning ANM. 1994. Development and dry matter distribution in glasshouse tomato: a quantitative approach. Doctoral dissertation, Wageningen Agricultural University, Wageningen, The Netherlands.

De Koning ANM. 1996. Quantifying the responses to temperature of different plant processes involved in growth and development of glasshouse tomato. *Acta Horticulturae* **406**, 99-104.

De Koning ANM. 2000. The effect of temperature, fruit load and salinity on development rate of tomato fruit. *Acta Horticulturae* **519**, 85-94.

Demetriades-Sha TH, Fuchs M, Kanemasu ET, Filocroft I. 1992. A note of caution concerning the relation between cumulated intercepted solar radiation and crop growth. *Agricultural Forestry Meteorology* **58**, 193-207.

Dewar RC. 1996. The correlation between plant growth and intercepted radiation: An interpretation in terms of optimal plant nitrogen content. *Annals of Botany* **78**, 125-136.

Dieleman JA. Heuvelink E. 1992. Factors affecting the number of leaves preceding the first inflorescence in the tomato. *Journal of Horticultural Science* **67**, 1-10.

Dinar M, Stevens MA. 1981. The relationship between starch accumulation and soluble solids content in tomato fruits. *Journal of the American Society for Horticultural Science* **106**, 415-418.

Dorais M, Demers DA, Papadopoulos A, Ieperen, W van. 2001 In: Janick J. ed. Greenhouse tomato fruit cuticle cracking. *Horticultural Reviews **30***, 163-168. *New York : Wiley and Sons, Inc.*

Dukes MD, Scholberg JM, Hanselman TA. 2005. Quantification of nitrogen movment under drip irrigated vegetable production. *Transactions of American Society of Agricultural Engineers* (ASAE) paper number **052240,** Anual International Meeting Tampa Fl, 17-20 July 2005.

Dumas Y. 1990. Tomatoes for processing in 90s: nutrition and crop fertilization. *Acta Horticulturae* **227**, 115-266.

Duvick DN. 1986. Plant breeding past achievements and expectations for the future. *Economic Botany* **40**(3), 289-297.

Ehret DL, Ho LC. 1986. Effect of salinity on dry matter partitioning and growth in tomato grown in nutrient film culture. *Journal of Horticultural Science* **61**, 361-367.

Ehret DL, Ho LC. 1986. Effects of osmotic potential in nutrient solution on diurnal growth of tomato fruit. *Journal of Experimental Botany* **37**, 1294-1302.

Enriquez LJ, Mercado Silva E, Castano Tostado E. 2005. Effect of two greenhouse covers on growth, dry matter content and tomato fruit quality. *Acta Horticulturae* **697**, 481-484.

Erdal I, Ertek A, Sengygit U, Yilmaz HI. 2006. Effects of different irrigation programs and nitrogen levels on nitrogen concentration, uptake and utilization of in proccesing tomatoes (*Lycopersicon esculentum*). *Australian Journal of Experimental Agriculture* **46**, 1653-1660.

Erickson RO. 1976. Modeling of plant growth. *Annual Review of Plant Physiology* **27**, 407-434.

Eshed Y, Zamir D. 1995. An introgression line population of *Lycopersicon pennellii* in the cultivated tomato enables the identification and fine mapping of yield associated QTL. *Genetics* **141**(3), 1147-1162.

Evans JR. 1989. Photosynthesis and nitrogen relationships in leaves of C_3 plants. *Oecologia* **78**, 9-19.

Farrar JF. 1988. Temperature and the partitioning and translocation of carbon. In: Long SP, Woodward FI, eds. *Plants and temperature*. 42th. Symposium of the society for Experimental Biology. Cambridge: Company of Biologists, pp 203-235.

Fernandez Munoz R, Cuartero J. 1991. Effects of temperature and irradiance on stigma exertion, ovule viability and embryo development in tomato. *Journal of Horticultural Science* **66**, 395-401.

Ferreira ME, Abreu JP, De Bianco VV, Monteiro A. 1997. Predicting phasic development of green beans for processing using a model with high temperature reduction of thermal time accumulation. *Scientia Horticulturae* **69**, 123-133.

Fishman S, Genard M. 1998. A biophysical model of fruit growth: simulation of seasonal and diurnal dynamics of mass. *Plant cell and Environment* **21**, 739-752.

Fleisher DH, Logendra LS, Moraru C, Both AJ, Cavazzoni J, Gianfagna T, Lee T, Janes HW. 2006. Effect of temperature perturbations on tomato (Lycopersicon esculentum Mill.) quality and production scheduling. *Journal of Horticultural Science and Biotechnology* **81**(1), 125-131.

Folker E. 1979. Commercial Production. In Folker E, ed. *The tomato. Study of the plant and the commercial production*. Buenos Aires, Argentina: Hemisferio Sur, pp 37-90.

Foolad MR. 2005. Breeding for abiotic stress tolerances in tomato. In: Ashraf M, Harris PJC, eds. *Abiotic Stresses: Plant Resistance through Breeding and Molecular Approaches*. New York: The Haworth Press, 613-684.

Foolad MR. 2007. Genome mapping and molecular breeding of tomato. *International Journal of Plant Genomics* **Vol. 2007**, 1-52.

Frary A, Nesbitt TC, Grandillo S, Van der Knaap E, Cong B, Liu J, Meller J, Elber R, Alpert KB. 2000. *fw*2.2: a quantitative trait locus key to the evolution of tomato fruit size. *Science* **289**, 85-88.

Fridman E, Pleban T, Zamir D. 2000. A recombination hotspot delimits a wild species quantitative trait locus for tomato sugar content to 484 bp within an invertase gene. *Proceeding of the National Academy of Sciences of the United States of America* **97**(9), 4718-4723.

Fujita K, Lei K, Saneoka H, Moghaieb REA, Mohapatra PK. 2004. Effect of N-deficiency on photoassimilate partitioning and rhytmic changes in fruit and stem diameter of tomato (*Lycopersicon esculentum*) during fruit growth. Proceedings of the 4th International Crop Science Congress. Brisbane, Australia, Sep 26-Oct 1 2004.

Garcia DM, Petzall CK, Castrillo M. 2004. Respuestas al deficit hidrico en las variedades de tomate Rio Grande y Pera Quibor. *Agronomy Tropical* **54** (4), 1-35.

Gardner FP. 1985. Photosynthesis. In: Gardner FP, Pearce RB, Mitchell RL, eds. *Physiology of crop plants*. Iowa. State University Press Ames, pp 3-29.

Garnier E, Berger A. 1986. Effects of water stress on stem diameter changes of peach growing in the field. *Journal of Applied Ecology* **23**, 193-199.

Gary C, Baille A, Navarrete M, Epanet R. 1997. TOMPOUSSE, un modele simplifie de prevision du rendement et du caliber de la tomate. In: Baille A, ed, Actes du seminaire de I'AIP intersectorielle "Serres", INRA, Avignon, pp 100-109.

Gary C, Jones JW, Longuenesse JJ. 1993. Modelling daily changes in specific leaf area of tomato: the contribution of the leaf assimilate pool. *Acta Horticulturae* **328**, 205-210.

Gary C, Tchamitchian M, Bertin N, Boulard T, Baille A, Charasse L, Rebillard A, Cardi JP, Marcelis LFM. 1998a. SIMULSERRE: education software simulating the greenhouse-crop systems. *Acta Horticulturae* **456**, 451-458.

Gary C, Jones JW, Tchamitchian M. 1998b. Crop modelling in horticulture: state of the art. *Scientia Horticulturae* **74**, 3-20.

Gary C, Barezi JF, Bertin N, Tchamitchian M. 1995. Simulation of individual organ growth and development on a tomato plant: a model a user- friendly interface. *Acta Horticulturae* **399**, 199-205.

Genard M, Huguet JG. 1996. Modeling the response of peach fruit to water stress. *Tree Physiology* **16**, 407-415.

Georgelis N, Scott JW, Baldwin EA. 2004. Relationship of tomato sugar concentration with physical and chemical traits and linkage of RAPD markers. *Journal of the American Society for Horticultural Science* **129**(6), 839-845.

Gijsman AJ, Hoogenboom G, Parton WJ, Kerridge PC. 2002. Modifying DSSAT crop models for low input agricultural systems using a soil organic matter residue module from CENTURY. *Agronomy Journal* **94**, 462-474.

Gijzen H, Goudriaan J. 1989. A flexible and explanatory model of light distribution and photosynthesis in row crops. *Agricultural Forestry Meteorology* **48**, 1-20.

Gijzen H. 1992. Simulation of photosynthesis and dry matter production of greenhouse crops. Simultion Reports CABO-TT **28**, Wageningen, The Netherlands.

Gijzen H. 1995. Interaction between CO_2 and water loss. In: Baker JC, Bot GPA, Challa H, Van de Braak NJ, eds. *Greenhouse climate control, an integrated approach*, The Netherlands: Wageningen Press, pp 51-62.

Gijzen H, Heuvelink E, Challa H, Marcelis LFM, Dayan E, Cohen S, Fuchs M. 1998. Hortsim: A model for greenhouse crops and greenhouse climate. *Acta Horticulturae* **456**, 441-450

Gillaspy G, Ben-David H, Gruissem W. 1993. Fruits: A developmental perspective. *The Plant Cell* **5**, 1439-1451.

Gimenez C, Mitchell VJ, Lawlor DW. 1992. Regulation of photosynthetic rate of two sunflower hybrids under water stress. *Plant Physiology* **98**, 516-524.

Goudriaan J, Monteith JL. 1990. A mathematical function for crop growth based on light interception and leaf area expansion. *Annals of Botany* **66**, 695-701.

Grange RI, Andrews J. 1993. Growth rates of glasshouse tomato fruit in relation to final size. *Journal of Horticultural Science* **68,** 747-754.

Grandillo S, Tanksley SD. 1996. QTL analysis of horticultural traits differentiating the cultivated tomato from the closely related species *Licopersicon pimpinellifolium*. *Theoretical and Applied Genetic*. **92**(8), 935-951.

Grandillo S, Ku HM, Tanksley SD. 1999. Identifying the loci responsible for natural variation in fruit size and shape in tomato. *Theoretical and Applied Genetic*. **99,** 978-987.

Grierson D, Kader AA. 1986. Fruit ripening and quality. In: Atherton JG, Rudich J, eds. *The Tomato Crop: A Scientific Basis for improvment*. London: Chapman & Hall, pp 241-280.

Guichard S, Gary C, Longuenesse JJ, Leonardi C. 1999. Water fluxes and growth of greenhouse toomato fruits under summer conditions. *Acta Horticulturae* **507**, 223-230.

Guichard S, Bertin N, Leonardi C, Gary C. 2001. Tomato fruit quality in relation to water and carbon fluxes. *Agronomie* **21**, 385-392.

Guichard S, Gary C, Leonardi C, Bertin N. 2005. Analysis of growth and water relations of tomato fruits in relation to air vapor pressure deficit and plant fruit load. *Journal of Plant Growth Regulation* **24**, 201-213.

Grindlay DJC. 1997. Towards an explanation of crop nitrogen demand based on the optimization of leaf nitrogen per unit leaf area. *Journal Agricultural Science* **128**, 377-396.

Gustafson FG. 1926. Growth studies on fruits. *Plant Physiology* **1**(3), 265-172.

Gustafson FG. 1927. Growth studies on fruits an explanation of the shape of the growth curve. *Plant Physiology* **2**(2), 153-161.

Garcia DM, Petzall CK, Castrillo M. 2004. Respuestas al deficit hidrico en las variedades de tomate Rio Grande y Pera Quibor. *Agronomy Tropical* **54** (4), 1-35.

Haeder HE, Mengel K. 1972. Translocation and respiration of assimilates in tomato plants as influenced by K nutrition. *Z Pflanz. Boden* **131**, 139-147.

Harper LA, Pallas JE Jr., Bruce RR. Jones JB Jr. 1979. Greenhouse microclimate for tomatoes in the southeast. *Journal of the American Society for Horticultural Science* **104**, 659-663.

Hartman PL, Mills HA, Jones JB Jr. 1986. The influence of nitrate: ammonium ratios on growth, fruit development, and element concentration in '*Floradel'* tomato plants. J*ournal of the American Society for Horticultural Science* **111**(4), 487-490.

He C, Zhang Z. 2006. Modeling the relationship between tomato fruit growth and the effective accumulated temperature in solar greenhouse. *Acta Horticulturae* **718**, 581-587.

Hebbar SS, Ramachandrappa BK, Nanjappa HV, Prabhakar M. 2004. Studies of drip fertigation in field grown tomato (*Lycopersicon esculentum* Mill.). *European Journal of Agronomy* **21**, 117-127.

Heuvelink, E, Marcelis, LFM. 1989. Dry matter distribution in tomato and cucumber. *Acta Horticulturae* **260**, 149-157.

Heuvelink E, Bertin N. 1994. Dry Matter partitioning in a tomato crop: comparison of two simulation models. *Journal of Horticultural Science* **69**, 885-903.

Heuvelink E. 1995. Growth, development and yield of a tomato crop: periodic destructive measurements in a greenhouse. *Scientia Horticulturae* **61**, 77-99.

Heuvelink E, Buiskool RPM. 1995. Influence of source-sink interaction on dry matter production in tomato. *Annals of Botany* **75**, 381-389.

Heuvelink E. 1996. Tomato growth and yield: quantitative analysis and synthesis. Doctoral dissertation, Wageningen Agricultural University. The Netherlands.

Heuvelink, E. 1997. Effect of fruit load on dry matter partitioning in tomato. *Scientia Horticulturae* **69**, 51-59.

Heuvelink, E. 1999. Evaluation of a dynamic simulation model for tomato crop growth and development. *Annals of Botany* **83**, 413-422.

Heuvelink E, Bakker M, Stanghellini C. 2003. Salinity effects on fruit yield in vegetable crops: a simulation study. *Acta Horticulturae* **609**, 133-140.

Heuvelink E, Tijskens P, Kang MZ. 2004. Modelling product quality in horticulture: an overview. *Acta Horticulturae*. **654**, 19-25.

Heuvelink E. 2005. Developmental processes. In: Heuvelink E, ed. *Crop production science in horticulture, tomatoes.* Cambridge: CABI Publishing, pp 53-83.

Ho LC, Sjut V, Hoad GV. 1982. The effect of assimilate supply on fruit growth and hormone levels in tomato plants. *Journal of Plant Growth Regulation* **1**, 155-171.

Ho LC, Shaw AW, Hammond JBW, Burton KS. 1983 Source sink relationships and carbon metabolism in tomato leaves. *Annals of Botany* **52**, 365-372.

Ho LC, Sjut V, Hoad GV. 1983. The effect of assimilate supply on fruit growth and hormone levels in tomato plants. *Journal of Plant Growth Regulation* **1**, 155-171.

Ho LC. 1984. Partitioning of assimilates in fruiting tomato plants. *Journal of Plant Growth Regulation* **2**, 275-277.

Ho LC, Hewitt JD. 1986. Fruit development. In: Atherton JG, Rudich J, eds. *The tomato crop. a scientific basis for improvement.* London: Chapman and Hall, pp 201-239.

Ho LC, Grange RI, Picken AJ. 1987. An analysis of the accumulation of water and dry matter in tomato fruit. *Plant, Cell and Environment* **10**, 157-162.

Ho LC. 1988. Metabolism and compartmentation of imported sugars in sink organs in relation to sink strength. *Annual Review of Plant Physiology and Molecular Biology* **39**, 355-378.

Ho LC, Grange RI, Shaw AF. 1989. Source/sink regulation. In: Baker DA, Milburn J, eds. *Transport of photoassimilate*. London, pp 306-343.

Ho LC. 1992. Fruit growth and sink strength. In: Marshall, C, Grace J, eds. Fruit and seeds production. Aspects of development, environmental physiology and ecology. Cambridge University Press. SEB seminar series **47**, 121-124.

Ho LC. 1996. Tomato. In: Zamski E, Schaffer A, eds. *Photoassimilate distribution in plants and crops.* Source-sink relationships. New York: Dekker M Inc, pp 709-728.

Hochmuth GJ. 1994. Efficiency ranges for nitrate-nitrogen and potassium for vegetable petiole sap quick test. *HorTechnology* **4**, 218-222.

Houghtaling HB. 1935. A developmental analysis of size and shape in tomato fruits. Bull. *Torrey Botany Club* **62**, 243-252.

Huett DO. 1986. Response to nitrogen and potassium of tomatoes grown in sand culture. *Australian Journal of Experimental Agriculture* **26**, 133-138.

Huett DO, Dettmann EB. 1988. Effect of nitrogen on growth, fruit quality and nutrient uptake of tomatoes grown in sand culture. *Journal of Experimental Agriculture* **28**, 391-399.

Huett DO, Dettmann EB. 1991. Nitrogen response surface models of zucchini squash, haed lettuce and potato. *Plant and Soil* **134**, 243-254.

Hunt R. 1982. Plant Growth Curves: the functional approach to plant growth analysis. London: Edward Arnold ed. 248 pp.

Hurd RG. 1973. Long-day effects on growth and flower initiation of tomato plants in low light. *Annals of Applied Biology **73***, 221-8.

Hurd RG, Gay AP, Mountifield AC. 1979. The effect of partial flower removal on the relation between root, shoot and fruit growth in the indeterminate tomato. *Annals of Applied Biology* 93, 77-89.

Hurd RG, Thornley JHM. 1974. An analysis of the growth of young tomato plants in water culture at different light integrals and CO_2 concentrations. I. Physiological aspects. *Annals of Botany* **38**, 375-388.

Hurd RG, Graves CJ. 1984. The influence of different temperature patterns having the same integral in the earliness and yield of tomato. *Acta Horticulturae* **148**, 547-554.

Hussey G. 1963a. Growth and development in the young tomato. I. The effect of temperature and light intensity on growth of the shoot apex and leaf primordia. *Journal of Experimental Botany* **14**, 316-25.

Infostat. 2002. Infostat version 1.1 User's Guide. Nacional University of Cordoba, Cordoba Argentina.

Jamieson PD, Porte JR, Wilson DR. 1991. A test of the computer simulation model ARC-WHEAT1 on wheat crops grown in New Zeeland. *Field Crop Research* **27**, 337-350.

Janes HW, McAvoy RJ. 1991. Environmental control of a single-cluster greenhouse tomato crop. *HortTechnology* **1**, 110-114.

Johnson R, Dixon MA, Lee DR. 1992. Water relations of the tomato during fruit growth. *Plant, Cell and Environment* **15**, 947-953.

Jones JB Jr. 1999. Tomato Plant Culture. In: Jones JB Jr, ed. *Tomato plant culture: in the field, greenhouse and home garden*. Boca Raton Forida: CRC Press, pp 51-72.

Jones HG, Tardieu F. 1998. Modelling water relations of horticultural crops: a review. *Scientia Horticulturae* **74**, 21-46.

Jones JW, Dayan E, Allen LH, Van Keulen H, Challa H. 1991. A dynamic tomato growth and yield model (TOMGRO). *Transactions of American Society of Agricultural Engineers* (ASAE) **34**, 663-672.

Jones JW, Hoogenboom G, Porter CH, Boote KJ, Batchelor WD, Hunt LA, Wilkens PW, Singh U, Gijsman AJ. Ritchie JT. 2003. The DSSAT cropping system model. *European Journal of Agronomy* **18**, 235-265.

Khan AA, Sagar GR. 1969. Alteration of the pattern of distribution of photosynthetic products in the tomato by manipulation of the plant. *Annals of Botany* **33**, 753-752.

Kawabata S, Sasaki H, Sakiyama R. 2005. Role of transpiration from fruits in phloem transport and fruit growth in tomato fruits. *Physiologia Plantarum* **124**, 371-380.

Khamis A, Ismail Z, Haron K, Mohamed AT. 2005. Nonlinear growth models for modeling oil palm yield growth. *Journal of Mathematics and Statistics* **1(3)**, 225-233.

Khayat E, Ravad D, Zieslin N. 1985. The effects of various night-temperature regimes on vegetative growth and fruit production of tomato plants. *Scientia Horticulturae* **27,** 9-13.

Kinet JM, Hurdebise D, Parmentier A, Stainier R. 1978. Promotion of inflorescence development by growth substance treatment to tomato plant growth in insufficient light conditions. *Journal of the American Society for Horticultural Science* **103**, 724-727.

Kinet JM. 1987. Inflorescence development in tomato. Control by light, growth regulators and apical dominance. *Plant Physiology* (Life Science Advance) **6**, 121-127.

Kinet JM, Zime V, Linotte A, Jaacqmond BG. 1986. Resumption of cellular activity induced by cytokinin and gibberellin in treatments in tomato flowers targeted for abortion in unfavorable light conditions. *Physiologia Plantarum.* **64**, 67-73.

Lohar DP, Peat WE. 1998. Floral characteristics of heat-tolerant and heat-sensitive tomato (Lycopersicon esculentum Mill.) cultivars at high temperature. *Scientia Horticulturae* **73**, 53-60.

Lakso AN, Corelli Grappadelli L, Barbad J, Goffinet MC. 1995. An expolinear model of fruit growth pattern of the apple fruit. *Journal of Horticultural Science* **70**, 389-394.

Langton FA, Cockshull KE. 1997. Is stem extension determined by DIF or by absolute day and night temperatures? *Scientia Horticuturae* **69**, 229-237.

Larouche R, Gosselin A, Vezna LP. 1989. Nitrogen concentration and photosynthetic photon flux in greenhouse tomato production: I. Growth and development. *Journal of American Society for Horticulture Science* **114**, 458-461.

Lawlor DW. 1995. The effects of water deficit on photosynthesis. In: Smirnoff N, ed. *Environment and plant metabolism. Flexibility and acclimation*. Oxford: pp 129-160

Lawlor DW. 2002. Carbon and nitrogen assimilation in relation to yield: mechanisms are the key to understanding production systems. *Journal of Experimental Botany* **53**, 773-787.

Le Bot J, Andamowicz S, Robin P. 1998. Modeling plant nutrition of horticultural crops: a review. *Scientia Horticulturae* **74**, 47-82.

Lee DR, Dixon MA, Johnson RW. 1989. Simultaneous measurements of tomato fruit and stem water potential using *in situ* stem hygrometers. *Canadian Journal of Botany* **67**, 2352-2355.

Lee DR. 1990. A unidirectional water flux model of fruit growth. *Canadian Journal of Botany* **68**, 1286-1290.

Leonardi C, Baille A, Guichard S. 2000. Predicting transpiration of shaded and non shaded tomato fruits under greenhouse environments. *Scientia Horticulturae* **84**, 297-307.

Lescurret F, Genard M. 2005. A virtual peach fruit model simulating changes in fruit quality during the final stage of fruit growth. *Tree Physiology* **25**, 1303-1315.

Li SH, Huguet JG, Schoch PG, Orlando P. 1989. Response of peach tree growth and cropping to soil water deficit at various phenological stages of fruit development. *Journal of Horticultural Science* **64**, 541-552.

Liu J, Cong B, Tanksley SD. 2003. Generation and analysis of an artificial gene dosage series in tomato to study the mechanisms by which the cloned quantitative trait locus *fw2.2* controls fruit size. *Plant Physiology* **132**, 292-299.

Liu HF, Genard M, Guichard S, Bertin N. 2007. Model assisted analysis of tomato fruit growth in relation to carbon and water fluxes. *Journal of Experimental Botany* **58** (13), 3567-3580.

Longuenesse JJ, Gary C, Tchamitchian M. 1993. Modeling CO_2 exchanges of greenhouse crops: a matter of scales and boundaries. *Acta Horticulturae* **328**, 33-47.

Lorenz OA, Tyler KB. 1983. Plant tissue analysis of vegetable crops. In: Reisenauer HM, ed. *Soil and plant tissue testing in California*. Div of Agr. Sci., Univ. of California. Berkely: **Bul 1879,** 21-24.

Maher MJ. 1976. Growth and nutrient content of a glasshouse tomato crop grown in peat. *Scientia Horticulturae* **4**, 23-26.

MacArthur JW, 1934. Linkage groups in the tomato. *Journal of Genetics* **29**, 123-133.

MacArthur JW, Butler L. 1938. Size inheritance and geometric growth processes in the tomato fruit. *Genetics* **23**, 253-268.

Mapelli S, Froba C, Torti G, Zoressi G. 1978. Relationship between set, development and activities of growth regulators in tomato fruits. *Plant Cell Physiology* **19**, 1281-1288.

Marcelis LFM. 1992. The dynamics of growth and dry matter distribution in cucumber. *Annals of Botany* **69**, 487-492.

Marcelis LFM. 1993. Fruit growth and biomass allocation to the fruits in cucumber 1.Effect of fruit load and temperature. *Scientia Horticulturae* **54**, 107-121.

Marcelis LFM. Heuvelink E, Goudriaan J. 1998. Modelling biomass production and yield of horticultural crops: a review, *Scientia Horticulturae*. **74**, 83-111

Marcelis LFM, Gijzen H. 1998. Evaluation under commercial conditions of a model of prediction of yield and quality of cucumber fruits. *Scientia Horticulturae* **76**, 171-181.

Menary RC, van Staden J. 1976. Effect of phosphorus nutrition and cytokinins on flowering in the tomato *Lycopersicon esculentum* Mill. *Australian Journal of Plant Physiology* **3**, 201-203.

Mills HA, Jones JB Jr. 1996. Plant analysis handbook II. Athens, GA: MicroMacro Publ. Inc., 422 pp.

Mitchell JP, Shennan C, Grattan SR. 1991. Developmental changes in tomato fruit composition in response to water deficit and salinity. *Physiologia Plantarum* **83**, 117-185.

Monselise SP, Varga A, Bruinsma J. 1978. Growth analysis of tomato fruits, *Lycopersicon esculentum* Mill. *Annals of Botany* **42**, 1245-1247.

Monteiro AA. 1983. Tomato fruit growth in relation to methods of improving fruit setting. *Acta Horticulturae* **137**, 307-314.

Monteith JL. 1977. Climate and the efficiency of crop production in Britain. London: Phil. Trans. Royal Soc., **281**, 277-294.

Monteith JL. 1994. Validity of the correlation between intercepted radiation and biomass. *Agriculture and Forestry Meteorology* 68, 213-220.

Moore EL, Thomas W. 1952. Some effects of shading and parachloro-phenoxy acetic acid on fruitfulness of tomatoes. Proc. *American Society Horticultural Science* **60**, 289-294.

Mossler M, Aerts MJ, Nesheim N. 2005. Florida crops. Pest management profiles.Tomatoes. University of Florida, *IFAS Extension* CIR **1238**, 1-19.

Nesbitt TC, Tanksley SD. 2001. *fw* 2.2 directly affects the size of developing tomato fruit, with secondary effects on fruit number and photosynthate distribution. *Plant Physiology* **127**, 575-583.

Nitsch JP. 1953. The physiology of fruit growth. Annual Review Plant Physiology and Molecular Biology **4,** 199-236.

Nuez F. 1995. Cultivo del tomate. Nuez F, ed, Madrid, Spain: Mundi-prensa, 796 pp.

Nyabundi JO, Hsiao TC. 1989. Effects of water stress on growth and yield of field grown tomatoes. I. Canopy development and biomass accumulation. *East Africa Agriculture and Forestry Journal* **55**, 17-26.

Opara L. 1999. Fruit growth measurement and analysis In: Janick J, ed. *Horticultural Reviews* **24**, 480pp.

Ortega Farias S, Ben-Hur L, Valdez H, Paillan H. 2003. Effects of four water applications on yield and quality greenhouse tomatoes produced in spring summer. *Technical Agriculture* **63** (4) 36-42.

Papadopoulos AP. 1985. Plant spacing effects on photosynthetically active radiation interception and utilization by greenhouse tomatoes. Doctoral dissertation, University of Guelph, Ontario, Canada, 428 pp.

Papadopoulos AP, Ormrod DP. 1988a. Plant spacing effects on light interception by greenhouse tomatoes. *Canadian Journal of Plant Science* **68**, 1197-1208.

Papadopoulos AP, Ormrod, DP. 1988b. Plant spacing effects on photosynthesis and transpiration of the greenhouse tomato. *Canadian Journal of Plant Science* **68**, 1209-1218.

Papadopoulos AP, Ormrod DP. 1990. Plant spacing effects on yield of the greenhouse tomato. *Canadian Journal of Plant Science* **70**, 565-573.

Papadopoulos AP, Ormrod DP. 1991. Plant spacing effects on growth and development of the greenhouse tomato. *Canadian Journal of Plant Science* **71**, 297-304.

Papadopoulos AP, Parajasingham S. 1997. The influence of plant spacing on light interception and use in greenhouse tomato (*Lycopersicon esculentum* Mill.). A review. *Scientia Horticulturae* **69**, 1-29.

Pearce BD, Grange RI, Hardwick K. 1993. The growth of young tomato fruit. I. Effects of temperature and irradiance on fruit grown in controlled environment. *Journal of Horticultural Science* **68**, 1-11.

Perez Alfoncea F, Estan MP, Caro M, Guerrier G. 1993. Osmotic adjustment in *Lycopersicon esculentum* and *L. penellii* under NaCl and polyethylenglycol 6000 isoosmotic stresses. *Physiologia Plantarum* **87**, 493-498.

Perry KB, Wu Y, Sanders DC, Garrett JT, Decoteau DR, Nagata RT, Dufault RJ, Batal KD, Granberry DM, Mclaurin WJ. 1997. Heat units to predict tomato harvest in southeast USA. *Agriculture and Forest Meteorology* **84**, 249-254.

Picken AJF. 1984. A review of pollination and fruit set in the tomato (*Lycopersicon esculentum* Mill.) *Journal of Horticultural Science* **59**, 1-13.

Picken AJF, Hurd RG, Vince-Prue D. 1985. Lycopersicon esculentum. In: Halevy AH, ed, CRC *Handbook of flowering* Vol. **3**. Boca Raton, FL: CRC Press, pp 330-346.

Picken AJF, Stewart K , Klapwijk D. 1986. Germination and vegetative development. In: Atherton JG, Rudich J, eds, *The tomato crop. A scientific basis for improvement.*, London: Chapman and Hall, pp 111-166.

Pill WG, Lambeth VN. 1977. Effects of NH^+ and NO_3^- nutrition with and without pH adjustment on tomato growth, ion composition and water relations. *Journal of the American Society for Horticultural Science* **102**, 78-81.

Pill WG, Lambeth VN, Hinckley TM. 1978. Effect of N form and level on ion concentration, water stress and blossom end rot incidence in tomato. *Journal of the American Society for Horticultural Science* **103**, 265-283.

Popper KR. 1959. The logic of the scientific discovery. New York: Basic Books, Inc, 480 pp.

Pressman E, Peet MM, Pharr DM. 2002. The effect of heat stress on tomato pollen characteristics is associated with changes in carbohydrate concentration in the developing anthers. *Annals of Botany* **5**, 631-636.

Rhaman SM, Nawata E, Sakuratani T. 1999. Effect of water stress on growth, yield and eco physiological responses of four tomato (Lycopersicon esculentum Mill.) cultivars. *Journal of the Japanese Society for Horticultural Science* **68** (3), 499-504.

Rinaldi M, Ventrella D, Gagliano C. 2007. Comparison of nitrogen and irrigation strategies in tomato using CROPGRO model. A case study from Southern Italy. *Agricultural Water Managment* **87**, 91-105.

Ritchie JT. 1998. Soil water balance and plant water stress. In: Tsuji GY, Hoogenboom G, Thornton PK, eds. *Understanding options for agricultural production*. Dordrecht, The Netherlands: Kluwer Academic Publishers, pp 41-53

Rylsky I. 1979. Fruit set and development of seeded and seedless tomato fruits under diverse regimes of temperature and pollination. *Journal of the American Society for Horticultural Science* **104**, 835-838.

Sachs RM, Hackett WP. 1969. Control of vegetative and reproductive development in seed plants. *HortScience* **4**, 103-107.

Sandri MA, Andriolo JL, Witter M. Dal Roos T. 2003. Effect of shading on tomato plants grown under greenhouse. *Horticulture Brasileira* **21** (4), p.642-645.

Sauviller C, Baets W, Pien H, Lemeur R. 2002. Simultom: a diagnostic tool for greenhouse tomato production. *Acta Horticulturae* **593**, 219-226.

Saw AF, Grange RI, Ho LC. 1986. The regulation of source leaf assimilate compartmentation. In: Cronshaw J, Lucas WJ, Guiaquinta RT, eds, *Plant biology phloem transport*, Vol. **1**. New York: AR Liss, pp 391-398.

Sawhney VK. 1983. The role of temperature and its relationship with gibberellic acid in the development of floral organs of tomato (Lycopersicon esculentum). *Canadian Journal of Botany* **61**, 1258-1265.

Sawhney VK, Dabbs DH. 1978. Gibberellic acid induced multilocular fruits in tomato and the role of Iocule number and seed number in fruit size. *Canadian Journal of Botany* **56**, 2831-2835.

Sawhney VK, Polowick PL. 1984. Fruit development in tomato: the role of the temperature. *Canadian Journal of Botany* **63**, 1031-1035.

Scott JW, Bryan HH, Ramos LJ. 1997. High temperature fruit setting ability of large-fruited, jointless pedicel tomato hybrids with various combinations of heat tolerance. *Proceedings of the Florida State Horticultural Society* **110**, 281-284.

Scott JW, Francis DM, Miller SA, Somodi GC, Jones JB. 2003. Tomato bacterial spot resistance derived from PI114490; inheritance of resistance to race T2 and relationship across three pathogens races. *Journal of the American Society for Horticultural Science* **128** (5), 698-703.

Scholberg JMS. 1996. Adaptive use of crop growth models to simulate the growth of field grown tomato. Doctoral dissertation, Graduate School of the University of Florida. Gainesville Fl.

Scholberg JMS, Boote KJ, Jones JW, McNeal BL. 1997. Adaptation of the CROPGRO model to simulate the growth of field-grown tomato. In: Kropff MJ, Teng PS, Aggarwal PK, Bouma J, Bouman BAM, Jones JW, van Laar HH, eds. *Systems approaches for sustainable agricultural development: Aplications of systems approaches at the field Level*. Dordrecht, The Netherlands: Kluwer Academis Publishers, pp 133-151.

Scholberg JMS, McNeal BL, Boote KJ, Jones JW, Locasio SJ, Olson SM. 2000. Nitrogen stress effects on growth and nitrogen accumulation by field-grown tomato. *Agronomy Journal* **92**, 159-167.

Schuarz D, Klaring HP, van Iersel MW, Ingram KT. 2002. Growth and photosynthetic response of tomato to nutrient solution concentration at two light levels. *Journal of American Society for Horticultural Science* **127** (6), 984-990.

Seeney DW, Graetz DA, Bottcher AB, Locascio SJ, Campbell KL. 1987. Tomato yield and nitrogen recovery as inflenced by irrigation method, nitrogen source, and mulch. *HortScience* **22**, 27-29.

Szymkowiak EJ, Sussex IM. 1992. The internal meristem layer (L3) determines floral meristem size and carpel number in tomato periclinal chimeras. *Plant and Cell* **4**, 1089-1100.

Steel R, Torrie J. 1992. Biostatistic: Principles and Procedures. Steel R, Torrie J. ed. New York: McGraw-Hill, 633 pp.

Struik PC, Yin X, de Visser P. 2005. Complex quality traits: now time to model. *Trends in Plant Science* **10**(11), 513-516.

Taber HG. 2001. Petiole sap nitrate sufficiency values for fresh market tomato production. *Journal of Plant Nutrition* **24**, 945-959.

Tanaka A, Fuyita K, Kikushi K.1974. Nutrio-physiological studies on the tomato plant. III. Photosynthetic rate of individuals leaves in relation to the dry matter production of plant. *Soil Science and Plant Nutrition* Soil **20**, 173-183.

Tanaka A, Fuyita K. 1974. Nutrio-Physiological studies on the tomato plant. IV. Source-sink relationship and structure of the source sink unit. *Soil Science and Plant Nutrition* **20**, 305-315.

Thornley JHM. 2006. Agriculture Modelling: a possible road map. Journal *of Agricultural Science* **144**, 446-449.

Torrecillas A, Guillaume C, Alarcon JJ, Ruiz Sanchez MG. 1995. Water relations of two tomato species under water stress and recovery. *Plant Science* **105,** 169-176.

Tyree MT, Hammel HT. 1972. The measurement of the turgor pressure and the water relation of plants by the pressure bomb technique. *Journal of Experimental Botany* **23**, 267-282.

Uzun S. 2006. The quantitative effects of temperature and light on the number of leaves preceding the first fruiting inflorescence on the stem of tomato (*Lycopersicon esculentum* Mill.) and aubergine (*Solanum melogena* L.). *Scientia Horticulturae* **109**, 142-146.

Vallejos CE, 1991. Low night temperatures have a differential effect on the diurnal cycling of gene expression in cold sensitive and tolerant tomatoes. *Plant, Cell Environment* **14**, 105-112.

Van Der Ploeg A, Heuvelink E. 2005. Influence of sub-optimal temperature on tomato growth and yield: a review. *Journal of Horticultural Science and Biotechnology* **80** (6), 652-659.

Van Ieperen W, Van Meeteren U, Oosterkamp J, Trouwborst G. 2005. Macro and microscopic aspects of fruit water relations influencing growth and quality in Tomato. *Acta Horticulturae* **682** (1) 501 -505.

Varga A, Bruinsma J. 1986. Tomato. In CRC Handbook of fruit set and development, Monselise SP, ed. Boca Raton, Fl: CRC Press, pp 461-480.

Verkerk K. 1955. Temperature, light and the tomato. *Mededelingen van de Landbouwhogeschool*. Wagenegein, **55**, 175-224.

Walker AJ. Ho LC. 1977. Carbon translocation in the tomato carbon import and fruit growth. *Annals of Botany* **41**, 813-823.

Wallach D. 2006. Evaluating crop models. In: Wallach D, Makowski D, Jones JW, eds. *Working with dynamic crop models.* Amsterdam, The Netherlands: Elsevier, pp 11-53.

Wang F, Sanz A, Brenner ML, Smith A. 1993. Sucrose synthase, starch accumulation, and tomato fruit sink strength. *Plant Physiology* **101**, 321-327.

Warner J, Zhang TQ, Hao X. 2004. Effects of nitrogen fertilization on fruit yield and quality of processing tomatoes. *Canadian Journal of Plant Science* 84, 865-871.

Warnock SJ, Isaacs RL. 1969. A linear heat unit system for tomatoes in California. *HortScience* **5**, 670-671.

Warnock SJ. 1973. Tomato development in California in relation to heat unit accumulation. *HortScience* **8**(6), 487-488.

Warren GF. 1998. Spectacular increases in crop yields in the United States in the twentieth century. *Weed Technology* **12**(4), 752-760.

Went FW. 1945. II Thermoperiodicity in growth and fruit of tomato. *American Journal of Botany* **31**, 135-150.

Willmott CJ. 1981. On the validation of models. *Physical Geography* **2**, 184-194.

Wilson WJ, Hand DW, Hannah MA. 1992. Light interception and photosynthetic efficiency in some glasshouse crops. *Journal of Experimental Botany* **43**, 363-373.

Winsor G, Adams P. 1987. *Glasshouse Crops*. Vol. **3**, 119-125.

Wittwer SH, Aung LH. 1969. Lycopersicon esculentum Mill. In: Evans LT, ed. The *induction of Flowering*. *Some Case Histories*. Melbourne, Australia: Macmillan pp 409.

Wolf S, Rudich J. 1988. The growth rate of fruits on different part of the tomato plant and the effect of water stress on dry weight accumulation. *Scientia Horticulturae* **34**, 1-11.

Ya Ling L, Marcelis LFM, Stanghellini C. 2004. Plant water relations as affected by osmotic potential of the nutrient solution and potential transpiration in tomato (*Lycopersicon esculentum* Mill.). *Journal of Horticultural Science and Biotechnology* **79** (2), 211-218.

Yeager AF. 1927. Determinate growth in tomato. *Journal of Heredity* **18**(6), 263-265.

Yoshioka H, Takahasi K. 1981. Studies on the translocation and accumulation of photosynthates in fruit vegetables. V. Translocation of photosynthates in a day, and effects of light conditions and night temperature on translocation and distribution of ^{14}C-photosynthates in tomato plants. Bull. *Vegetables Crops*. Sta. Japan: **A9**, 63-81.

Young PA, MacArthur JW. 1947. Horticultural characters of tomato. Texas Agric. Expt. Sta. Bul. **698**, 1-61.

Zeng ZB, Houle D, Cockreham CC. 1990. How informative is Wright's estimator of the number of genes affecting a quantitative character? *Genetics* **26**, 235-248.

BIOGRAPHICAL SKETCH

M. Raquel Rybak was born in Leandro N. Alem, Misiones, Argentina. She is the daughter of Veronica Kuyesen and Jose Rybak.

Raquel graduated from the National University of the Northeast in Corrientes, Argentina, in 1995 with the Agricultural Engineer degree. In 1996 she began to work in the National Institute of Agricultural Technology (INTA). In 1998 she was awarded a fellowship to pursue graduate studies in the University of Concepcion, Chillan, Chile. She graduated with the master's degree in agricultural engineering with specialization in Irrigation and Drainage in 2001.

In 2005 she was awarded a fellowship from INTA to pursue graduate studies in the United States. Raquel enrolled at the University of Florida in summer 2005 with Dr. Kenneth Boote as her adviser. She received her Ph.D. from the University of Florida in the spring of 2009. At the end of her studies she reassumed her position in INTA, Argentina.

Raquel is a member of the Professional Council of Agricultural Engineers (CPIA), American Society of Agronomy and Crop Science Society of America. She is also a member of the honor Society of Agriculture Gamma Sigma Delta.